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ECOLOGY OF THE MICROSCOPIC METAZOA INHABITING THE SANDY BEACHES OF SOME WISCONSIN LAKES[1]

By

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[1] The greater portion of this investigation served as the basis for a thesis presented to the Graduate School of the University of Wisconsin in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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INTRODUCTION

Sandy Beaches as an Environment

In the mind of the biologist "sand" is almost invariably associated with "lifelessness" and "desert." However, when consideration is given to the sandy beaches which border so many fresh water lakes, such a conception is far from the truth. Recent work in Russia, Poland, and the United States has served as an introduction to the realization that a complex microscopic flora and fauna inhabit the capillary water held between the sand grains of such beaches. This is especially true of the uppermost 3 cm. of the sand within 250 cm. of the water's edge.

In spite of the fact that a beach environment is a heterogeneous mixture of sand grains, air, water, and organic debris, the organisms found there are primarily of the genera and species encountered in true littoral situations. Rotatoria are the dominant Metazoa, but large numbers of Copepoda and Tardigrada are often present. Nematodes, gastrotrichs, insect larvae, and turbellarians are common but not abundant. Enormous numbers of Protozoa and algae serve to further crowd the available space. An optical section of a small portion of a beach showing the relative sizes of some of the more common Metazoa in relation to the sand grains is given diagrammatically in Figure 1.

Various workers have divided sandy beach areas into three parallel zones: (1) an inner beach, which extends from the water's edge as far back as the first signs of drying on the surface of the sand, (2) a middle beach, farther shoreward, over which waves wash only during rough weather, and (3) the outer beach, extending from the middle beach to the landward limit of the sand. Wiszniewski (1934) has applied the term "psammolittoral" to the sandy beach environment and has distinguished three areas: (1) the "hydropsammon," submerged sand along the edge of a body of water, (2) "hygropsammon," the area about one meter in width immediately above the lake's edge, almost constantly saturated with water by capillarity or wave action, and (3) the "eupsammon," corresponding in general to the middle beach. The present study is confined for the most part to the top 8 cm. of sand in the hygropsammon and eupsammon. In addition, many samples were taken from the submerged sand of the hydropsammon and from the outer beach for comparison.

In contrast to ordinary aquatic conditions, the psammolittoral organisms inhabit very unstable and unique surroundings largely on account of the

effects of factors outside the sand. The amount of capillary water may change markedly over a short period of time and during drying conditions the organisms become restricted to a smaller and smaller film of water. The range of temperature, even during the course of a single day, may be comparatively great. The amount of oxygen and carbon dioxide dissolved in the capillary water may fluctuate, depending on a number of agencies. The amount of available food material in the sand is decidedly inconstant. These factors, as well as others, have been investigated in order to ascertain their

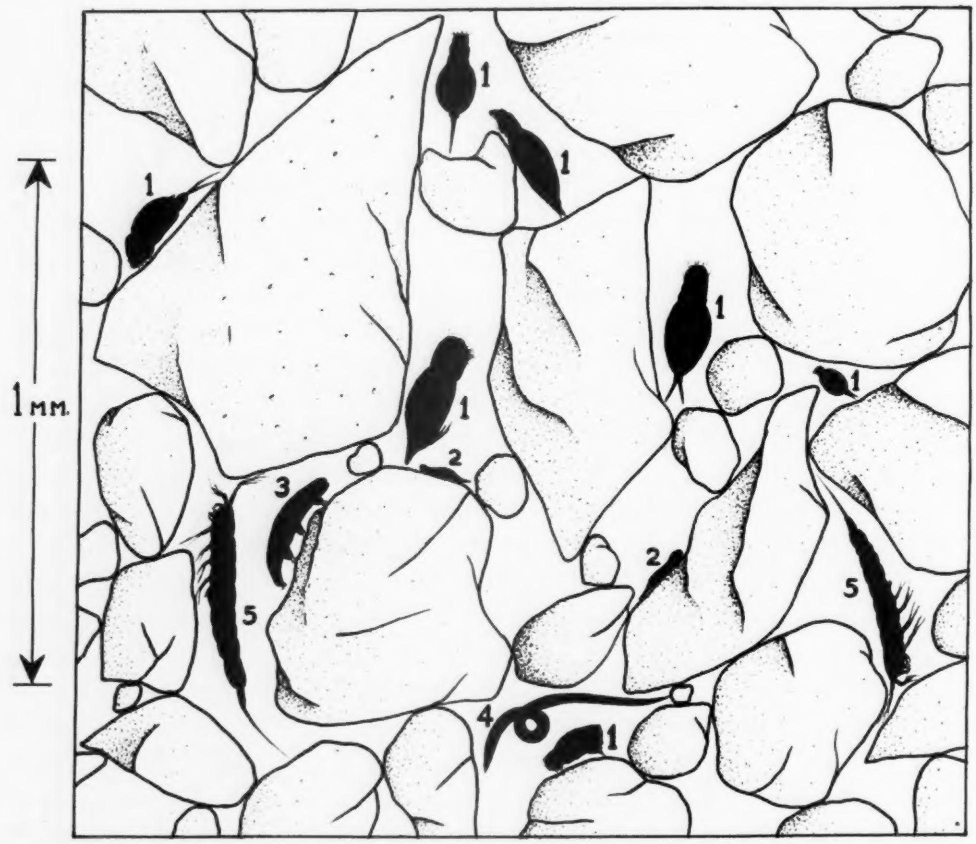


FIG. 1. Optical section of a small portion of a sandy beach showing relative sizes of sand grains and some of the common species of microscopic Metazoa. 1 = rotifers, 2 = gastrotrichs, 3 = tardigrade, 4 = nematode, 5 = harpacticoid copepods. (After Pennak, 1939b).

effects upon the numbers and distribution of organisms in sand. It is the plan of this paper to present short discussions of physical and chemical conditions in beaches, and a more extensive treatment of the psammolittoral metazoans in relation to these conditions.

LITERATURE

Although there is a large literature dealing with the macroscopic organisms inhabiting fresh water beaches, ocean beaches, and tidal flats, the microscopic fauna has been almost entirely neglected until recently. Wiszniewski

(1934a) has reviewed the literature concerned with sandy beaches so there is no need for such a discussion here. It is profitable, nevertheless, to cite some of the more significant works, especially those which have a direct bearing on the present study.

Attention was first drawn to sandy beaches by the late Dr. N. A. Cobb, nematologist of the United States Department of Agriculture, who discovered large numbers of copepods and nematodes in ocean beaches.

In 1926 Sassuchin presented a brief study of the Protozoa found on the sandy shores of the Oka River, Russia. In the following year Sassuchin, Kabanov, and Neiswestnova published a longer report on the microflora and fauna inhabiting a beach of the same river. They listed algae, Protozoa, Rotatoria (21 species), and a few other groups, with remarks concerning the relative abundance of the various species in the restricted area studied. A small amount of chemical and physical data was also given.

Bruce (1928, 1928a) has considered the physical and chemical factors in the ocean beaches at the Plymouth Biological Station in England.

Wilson (1932) reported the occurrence of many species of copepods from the ocean beaches in the Woods Hole region, and in 1935 he published a general account of the biology of this particular group. Continuing along the same lines, Nicholls (1935) in Scotland, and Otto (1936), Schulz (1937), and Kunz (1938) in Germany have reported many new species of copepods from marine beaches.

In a brief note, Wiszniewski (1934) called attention to the importance of the sandy beach as an environment for microscopic life, and in the same year (1934a) he presented a general survey of the ecology of the psammolittoral of Lake Wigry and neighboring lakes in Poland with an account of the taxonomy of the Rotatoria found in those beaches. More recently, this author has published a series of short papers on the biology of the Rotatoria inhabiting sandy beaches of lakes and rivers at various locations, mostly in Poland (1934b to 1937a). Stangenberg (1934) presented data on the chemistry of the capillary water at two beaches on the shore of Lake Wigry.

In this country, Myers (1936) listed the species of rotifers found in the psammolittoral of two acid lakes in New Jersey, and Pennak (1939b) presented a summary of the ecology of the psammolittoral organisms with special emphasis on problems suitable for future investigation.

SCOPE OF THE WISCONSIN INVESTIGATIONS

The present investigation was undertaken during the summer months of 1936, 1937, and 1938 to study the ecology of the microscopic Metazoa (especially the Rotatoria, Copepoda, and Tardigrada) inhabiting the top 8 cm. of exposed sand on the shores of 15 Wisconsin lakes. Eleven of these lakes are situated in northeastern Wisconsin, two are at Madison, Wisconsin, namely Lakes Monona and Mendota, and the others are Lakes Superior and Michigan (Great Lakes). One beach was chosen for study at each of 11

lakes, two were chosen at each of three lakes, and three were chosen at the last lake, thus making 20 locations in all. On lake shores where only one beach was studied, that beach is hereinafter designated by the name of the lake; where two or three beaches were studied on the same lake they are designated according to their geographical position on the shore. Table 1 is a list of the locations investigated with dates on which the 66 series of sand samples were taken.

In addition to the collection of 2702 sand samples (comprising the 66

TABLE 1. LOCALITIES AND DATES OF COLLECTION OF SERIES OF SAND SAMPLES FROM WHICH ORGANISMS WERE REMOVED FOR STUDY

Beach	Dates of Collection			Total number of series of samples	Total number of individual sand samples
	1936	1937	1938		
Monona		June 28 Sept. 8 Oct. 29		3	144
Mendota	May 18 Sept. 1 Nov. 12	Apr. 16 May 7 May 14 May 28 June 4 June 22 Sept. 3 Oct. 8		11	616
Arbor Vitae	Aug. 5			1	48
Plum	July 22		Aug. 19	2	44
N. Trout	July 5 Aug. 16	July 4 July 18 Aug. 1 Aug. 17	July 3 July 31 Aug. 4 Aug. 26	10	407
S. Trout	July 19 Aug. 13	July 5 Aug. 15	July 12 Aug. 15	6	228
SW. Trout	July 19 Aug. 13	July 23		3	144
Michigan		May 29		1	56
Superior		Aug. 8	July 17	2	55
E. White Sand	July 22	July 18	July 24	3	119
NE. White Sand			Aug. 18	1	6
Boulder	Aug. 2	Aug. 14	July 24	3	69
NE. Muskellunge	July 16 Aug. 21	July 13 Aug. 22		4	224
E. Muskellunge			July 31 Aug. 13	2	12
Pallette	July 30	July 11	July 10	3	118
Weber	July 29 Aug. 11			2	96
Starrett		July 30	Aug. 7	2	46
Day	Aug. 2	July 27		2	88
W. Crystal	July 9			1	40
E. Crystal	July 9	July 8	July 3 Aug. 23	4	142
TOTAL				66	2702

series) from which the organisms were removed for enumeration and identification, certain physical and chemical observations were made at the beaches. The data on physical conditions include sand temperatures, amount of capillary water held in the sand, size of sand grains, slope of the beaches, amount of exposure and wave action, and the amount of particulate organic matter held in the interstices of the sand. A number of chemical determinations were carried out on the capillary water; these included pH determinations, free and bound carbon dioxide, dissolved oxygen, and organic and inorganic residues.

It is with great pleasure that the author takes this opportunity to express his indebtedness to Dr. B. G. Chitwood of the Nematology Division of the United States Department of Agriculture for the identification of a number of nematodes; to Drs. R. E. Coker of the University of North Carolina and C. B. Wilson of Westfield, Massachusetts, for advice and information on certain Copepoda; to F. J. Myers of Ventnor, New Jersey, for the identification of certain Rotatoria; to Dr. N. Sjolander and Mr. Nelson Rodgers for data on bacteria and Protozoa of several Wisconsin beaches; and especially to Professor C. Juday of the University of Wisconsin for his generosity in providing for the author the facilities necessary to carry on this investigation at the Trout Lake Limnological Laboratory of the Wisconsin Geological and Natural History Survey.

DESCRIPTIONS OF BEACHES STUDIED

During the course of this investigation an effort was made to include a variety of beaches, particularly with reference to the chemical characteristics of the lake waters, exposure to wave action, amount of organic matter in the sand, size of the sand grains, and slope of beach. In all cases locations were chosen which were not likely to be disturbed by human beings. Also, wide beaches were usually selected in order that a complete picture of the horizontal distribution of the organisms might be obtained. All of the beaches in northeastern Wisconsin are in Vilas County and within easy reach of the Limnological Laboratory at Trout Lake. Figure 2 shows the locations of these Vilas County beaches. The characteristics of all 20 beaches which were studied are briefly outlined below in order of decreasing hardness of the lake waters.

Monona. The beach studied at Lake Monona (area = 1410 ha.) is situated on the north shore near the west end within the city limits of Madison, Wisconsin. Although the beach at this point is exposed to the prevailing south and west winds during the summer months, there is not sufficient sweep of the lake to produce any considerable wave action. This beach was created artificially in the spring of 1936 by the dumping of large quantities of sand brought from a gravel pit. Although it was intended for a bathing beach, it received very little use as such. The location was chosen in order to observe the development of the psammolittoral population in a beach known

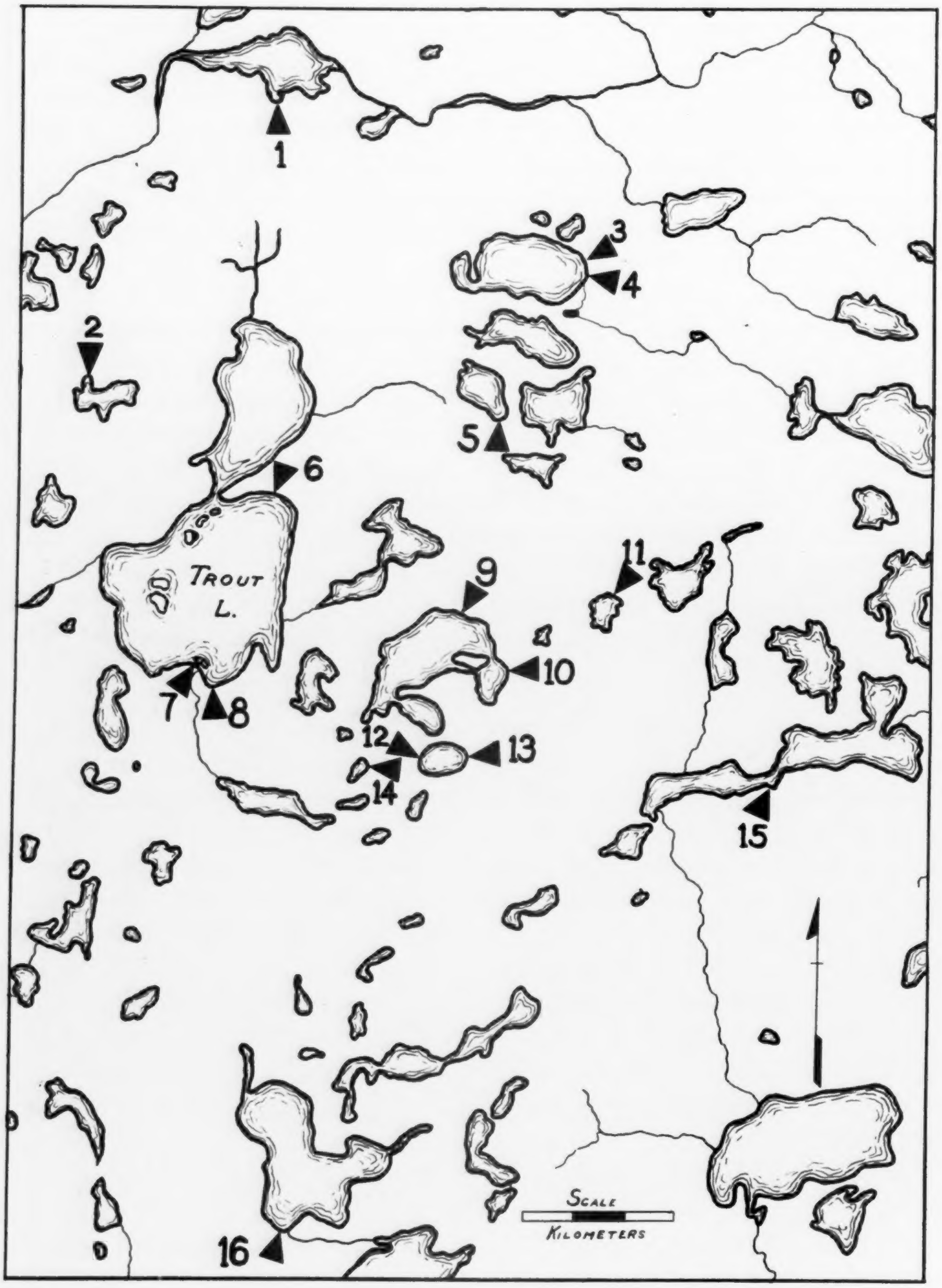


FIG. 2. Map of a portion of Vilas County, Wisconsin, showing the locations of sixteen of the beaches which were studied. 1 = Boulder, 2 = Day, 3 = NE. White Sand, 4 = E. White Sand, 5 = Pallette, 6 = N. Trout, 7 = SW. Trout, 8 = S. Trout, 9 = NE. Muskellunge, 10 = E. Muskellunge, 11 = Starrett, 12 = W. Crystal, 13 = E. Crystal, 14 = Weber, 15 = Plum, 16 = Arbor Vitae.

to be barren at a definite time in its history. The sand is of finer grade than the sand of the few natural beaches on the lake, and contained about 6% by volume of clay. In the foreground of Figure 3 where the samples were taken, the beach is about 15 m. in width, ending in a concrete retaining wall.

Mendota. This beach is also within the city limits of Madison, on the east shore of the lake (area = 3940 ha.). It is subject to vigorous wave action because of exposure to the west winds sweeping over a broad expanse of water. The sand particles range widely in size, from fine sand to coarse gravel. This is the only beach studied which contains fragments of mollusk shells in appreciable amounts. In the foreground of the accompanying photograph (Fig. 4) the distinct line of gravel is about 140 cm. from the water and the inner limit of the debris at the right is about 260 cm. from the water. Chemically, the lake is similar to Monona; bound carbon dioxide averages about 75 ppm.

Fig. 3. Beach on northwest shore of Lake Monona at Madison, Wisconsin.

Arbor Vitae. This lake is rather large (471 ha.) and medium hard. The beach studied is on the south shore and is composed of relatively homogeneous sand. It is quite narrow, being only about 180 cm. in width from the water's edge to a heavy growth of grasses at its outer limit.

Plum. Although Plum Lake is large, the beach selected is situated on a small protected bay on the south shore of a strait where there is very little

wave action. This was the narrowest beach studied, being 120 cm. in width and limited at its outer edge by the lawn of a summer resort. The sand particles are uniformly medium-sized and little organic matter was present.

N. Trout. Trout Lake, in Vilas County, is a moderately hard oligotrophic lake, having a bound carbon dioxide content of about 19.0 ppm. It is divided into two basins which are connected by a narrow channel. This particular beach is located just to the east of the Limnological Laboratory on the north shore of the larger south basin (area = 1683 ha.). It is subject to greater wave action than any of the other beaches studied except Superior. The inner limit of the grasses shown in the photograph is about 340 cm. from the water. On several occasions during the past four summers the waves, driven by fresh winds, have almost reached these grasses. Within a meter of the water the beach is gravelly.

FIG. 4. Beach at east end of Lake Mendota, Madison, Wisconsin.

S. Trout. This location is directly opposite the one just described, at the extreme south end of the lake. Except for this difference, these two locations are quite similar. They were chosen in order to detect any variations in the faunal distribution which might be due to the difference in exposure to wave action.

SW. Trout. The third location on Trout Lake is situated on the southwest shore and is protected by an island about 200 m. from the mainland.

Adjacent to this beach the lake is very shallow; as far as 100 m. from the shore it is only about 1 m. in depth. The bottom in this area is covered with a dense growth of potamogetons. The beach is comparatively narrow and contains a moderate amount of organic debris. Grasses appear at 150 cm. from the water and form a heavy growth at 200 cm. The sand particles are of small dimensions.

Michigan. One series of samples was taken on the shore of Lake Michigan near the southern limits of Milwaukee, Wisconsin. The beach is about 40 m. in width and is protected from severe wave action by a breakwater which runs parallel to the shore at a distance of 400 m. Near the water it is composed of gravel but landwards it merges into fine sand. Very little organic material is present.

Superior. Two series of samples were collected from the broad beach of Lake Superior in the Porcupine Mountain area 15 miles west of Ontonagon, Michigan. Even after prolonged periods of southerly winds there is a pronounced ground swell which rolls in upon this shore. Except near the water's edge where there is a large proportion of gravel, the sand is mostly fine and medium, containing scattered pebbles.

E. White Sand. Of the two beaches selected at the east end of White

FIG. 5. N. Trout beach. Situated on the north shore of the south basin of Trout Lake, Vilas County, Wisconsin. (After Pennak, 1939b).

Sand Lake, in Vilas County, this is the more southern. It is composed of coarse yellowish sand. A quantity of debris was usually present at a distance of 250 cm. from the water's edge.

NE. White Sand. This location is about 400 m. north of the one just mentioned and is similar to it except for the fact that it has a more gradual slope.

Boulder. Boulder Lake has highly colored water and few beaches, all of which are narrow. The beach studied is subject to almost no wave action since it is situated on the south shore and is protected by a dock about 40 m. from shore. It is shaded from the sun and wind by an overhanging dock.

NE. Muskellunge. Of the two beaches studied at Muskellunge Lake (area = 375 ha.), this one is on the northeast shore where it is often washed by moderate waves. The sand is of uniformly fine grain and the beach is about 260 cm. in width between the water's edge and the first line of grasses.

E. Muskellunge. The other beach on Muskellunge Lake is on the east shore in a protected location. It has a very abrupt slope and contains much organic material.

Pallette. Pallette Lake is a soft-water lake, having an area of 82 ha. The location chosen is on the south shore where the beach is about 10 m. in width and where there is little wave action. The sand consists of small, light-colored grains. All beaches hereinafter discussed are characterized by this type of sand.

Weber. This lake is the smallest one of the series, being only 18 ha. in area. It is oligotrophic, has a smooth outline, and low plankton productivity. The beach selected for study is at the east end. It is clean for about 150 cm after which there is a sparse growth of grasses.

Starrett. This lake has an area of 44 ha. In spite of its soft water it supports a large plankton population. The maximum depth is 7.5 m. The beach chosen on the east shore was found to contain more particulate organic material than any other location studied.

Day. Although this lake has an area of 60 ha., the location selected is well protected from waves since it is situated on a small arm of the main body of water at the extreme north end of the lake.

W. Crystal. Crystal Lake has an area of 37 ha. and is ovoid in outline. The water is very soft; bound carbon dioxide averages only 1.4 ppm. Plankton production is low. Of the two beaches selected at this lake, W. Crystal is at the west end. Here a clean beach slopes away from the water's edge for 50 cm. and at that distance rises abruptly to a height of 14 cm., forming a miniature plateau overgrown with grasses.

E. Crystal. In contrast to the west shore of Crystal Lake, this beach slopes away uniformly and gradually from the water's edge to form a beach about 20 m. in width. A line of grasses starts at about 200 cm. from the

water's edge. Both this beach and the one at the opposite end of the lake contained a small amount of organic debris.

METHODS

The samples for the enumeration of the organisms contained in the sand were collected at intervals from the 20 beaches studied. During 1936 and 1937, 10 cc. sand samples were used as units of study. They were taken in the following manner: at the water's edge and at various distances (stations) from the water's edge (usually 50 cm. intervals) brass tubes, each having an internal cross-sectional area of 10 cm.^{2}, were thrust vertically into the sand to a depth of 10 or 12 cm. Each tube was carefully removed and corked at both ends without disturbing the contained core of sand. These were taken back to the laboratory where the organisms were removed from the sand by washing. First, both corks were removed and a plunger inserted into the lower end of the tube. Then the core of sand was pushed out of the upper end where slices 1 cm. in thickness were cut off with a spatula and placed in 30 cc. shell vials. In this way eight successive 1 cm. layers of the sand core, each having a volume of 10 cc., were treated as separate samples. Each sample was well shaken four times with separate portions of lake water which were quickly decanted off into a large test tube containing a small amount of a narcotic solution. After being allowed to stand for about 10 minutes, 3 cc. of formalin was added. After another period of 10 minutes, by which time the dead organisms and debris had settled to the bottom of the test tube, most of the supernatant liquid was discarded and the residue transferred to a small vial to be examined at a later date. Tests showed that this washing and concentration method removed between 94 and 98% of the organisms from the sand samples.

During 1938 the sand cores were not divided horizontally, but the entire cores to a depth of 8 cm. were treated as single samples.

Except in a few cases no effort was made to take subsequent series of sand samples from precisely the same points on the beaches. However, in most instances they were taken within 5 m. of one another.

For counting, the contents of the vials were placed in a Sedgwick-Rafter chamber and the organisms on the entire slide were enumerated and identified. Specimens of uncertain identification were permanently mounted in glycerin for a more careful examination.

Frequently, a duplicate series of 10 cc. samples was taken in order to determine the amount of particulate organic matter in the sand at the various stations and depths. The organic matter was removed by the above washing method, dried in platinum crucibles at 60°C., and then ignited. The loss on ignition roughly represented the organic matter in the samples.

Also, duplicate series of samples were often taken to determine the amount of capillary water in the sand. This was done by weighing the in-

dividual wet sand samples in watch glasses, allowing to dry for 24 hours, and then reweighing.

Approximate temperatures of the sand were taken by thrusting tested laboratory thermometers to the appropriate depths and reading to 0.1°C.

For chemical determinations the capillary water was collected from the sand with a volumetric pipette or a simple suction flask arrangement by which water could be slowly sucked out of the sand through a piece of glass tubing thrust into the sand to a depth of 4 cm. Since the sand samples were taken to a depth of 8 cm., these water samples can be regarded as representing average conditions between the surface of the sand and a depth of 8 cm. A small piece of coarse silk bolting cloth was placed over the end of the tube to prevent the entrance of sand and debris. Each water sample (usually 150 cm.) was taken by sucking the water out of the sand at several neighboring points at each station in order that none of the capillary water below a depth of 8 cm. might be drawn up and contaminate the samples. The water was taken back to the laboratory in glass-stoppered bottles of 150 cc. capacity. Care was taken to fill the bottles to overflowing so that the introduction of the stopper would eliminate all air bubbles from the sample. In taking samples the chief difficulty was in sucking the water up slowly enough so that air bubbles from the sand would not become mixed in with the sample, thus rendering it useless for any dissolved gas determinations. Samples contaminated in such fashion were discarded. No samples could usually be taken farther back than 100 cm. from the water's edge because of the quantities of air in the sand beyond that distance. For comparison, samples of the lake water 25 cm. from the shoreline were sometimes taken.

Hydrogen ion determinations were made with a LaMotte colorimetric outfit. The usual Winkler method was used for dissolved oxygen analysis. Free and bound carbon dioxide were determined with N/44 sodium carbonate and phenolphthalein, N/44 HCl and methyl orange, respectively.

PHYSICAL FACTORS IN SANDY BEACHES

BEACH SLOPE

As will be shown later, the degree of slope of a beach fixes the horizontal extent of the organisms in the sand. On beaches with pronounced slopes the width of the beach which contains sufficient interstitial water for the organisms is comparatively narrow. Conversely, on flat beaches the sand is wet back far enough to permit psammolittoral organisms to live as much as 3 m. from the water's edge. Whenever sand collections were made the slope was measured in order that the horizontal distribution of the organisms might be correctly interpreted.

In general, winds and waves do not exert sufficient influence during the course of a summer to produce any marked variations in the slope. Variations are common within 100 cm. of the water's edge, but they have no

significant effects on the distribution of organisms there. Occasional storms and high winds, however, may radically change the slope farther back than that.

The range of beach slope found during this investigation was considerable. Figure 6 shows some of these data. The most gradual slope (approximately 2.5° from the horizontal) was found at E. Crystal on July 8, 1937 when the surface of the sand 150 cm. from the water's edge was only 6 cm. above lake level. E. Muskellunge, a wide beach, on July 31, 1938 had a pronounced slope (8.2°), the surface of the sand being 23 cm. above lake level 150 cm. from the water's edge. At the 200 cm. station it was 2 cm.

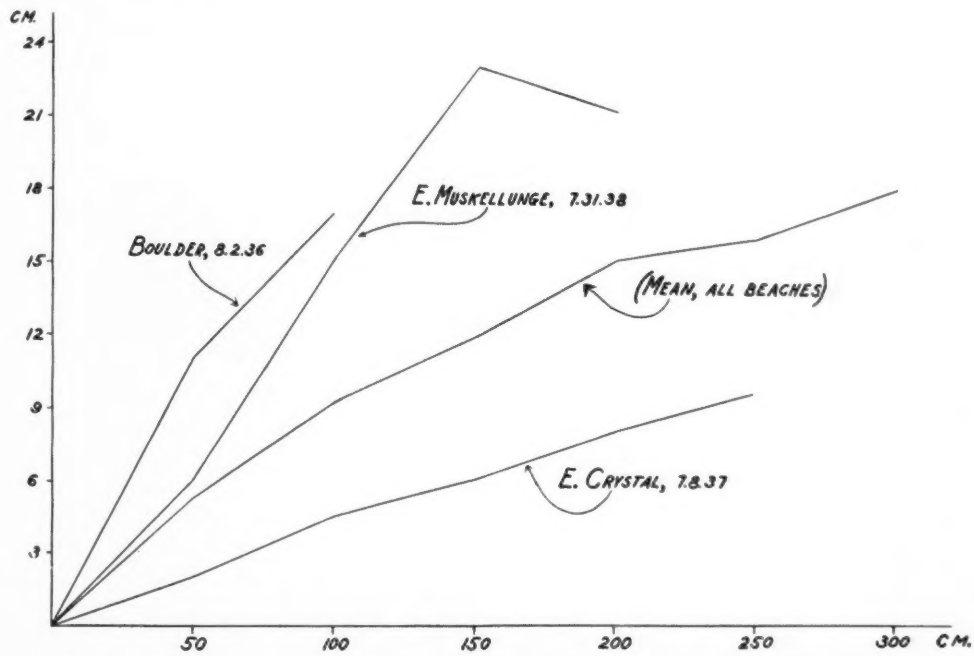


FIG. 6. Slope of several beaches. Vertical scale = height of surface of sand above lake level. Abscissae = distance from water's edge. Vertical scale exaggerated by a factor of 8.7.

lower; such a condition was common. Of the narrow beaches, Boulder, with a slope of 11.5° on August 2, 1936, represents an extreme condition. Figure 6 shows the mean slope for all measurements made during this study. Accordingly, an average beach might be said to be about 9 cm. above water level 1 m. from the water's edge and 15 cm. in height at a distance of 2 m., thus resulting in a slope of approximately 5°.

DISTRIBUTION OF GRADES OF SAND

The relative amounts of the different size sand grains were determined for most of the beaches by running the beach sand through a series of regulation woven brass wire Tyler sieves and weighing the sand retained by each sieve. Although the approved method requires the use of round mesh sieves,

especially for coarse material, this type was not available. Since the sand grains are for the most part not particularly angular, it is felt that these results are comparable with more exact work. In soils work it is customary to use the range 0.25-0.50 mm. as constituting medium sand particles and 0.50-1.00 mm. as being the limits of coarse sand. Although sieves were not available so that a separation corresponding to these ranges could be made, a somewhat similar separation into "gravel," "coarse," "medium," and "fine" sands was facilitated by the use of sieves numbered 16, 30, and 50. The data for the sieves used in this study are given in Table 2.

Cornish (1910) pointed out that breaking waves on a beach are responsible for a selective transportation of the finer grades in a shoreward direction and the accumulation of the coarser grades at and near the water's edge. This phenomenon was plainly visible at seven of the Wisconsin beaches. Figure 7 shows the horizontal weight distribution of four grades of sand at six of these locations. Superior had the greatest amount of gravel with approximately 35% at the 0, 100, and 200 cm. stations, where selectivity was only slightly apparent. Beyond 200 cm., however, the amount of gravel decreased to 6.1% and 1.2% at the 260 and 320 cm. stations, respectively. At S. Trout there was no selectivity in the first 100 cm. of beach, but between the 150 and 300 cm. stations the proportion of gravel and coarse sand decreased by one half and the amount of medium sand increased accordingly. Similarly, the first 200 cm. of N. Trout beach was comparatively homogeneous with about 40% gravel and coarse sand. Selectivity was apparent only at the 250 and 300 cm. stations where medium sand was much more abundant and the larger sizes fell to less than 10%. Mendota showed a plain case of selectivity; the composition varied from 38.2% gravel and coarse sand at the water's edge to 3.3% at the 250 cm. station and a corresponding increase in fine and medium sands. An unusual situation appeared at Monona, where 31.8% of gravel and coarse sand was found at the water's edge, less than 1% at both the 100 and 150 cm. stations, and an increase to 13.1% at the 250 cm. station. This distribution was probably due to the youth of the

TABLE 2. TYLER STANDARD SIEVES; MEASUREMENTS

U. S. series equivalent	Meshes per inch	Size of openings		Grade of sand retained
		inches	mm.	
12	10	.065	1.65	
16	14	.046	1.17	"gravel"
20	20	.033	.83	
30	28	.023	.59	"coarse" sand
40	35	.016	.42	
50	48	.012	.30	"medium" sand
70	65	.008	.21	
(particles passing No. 50 sieve)				"fine" sand

beach, since wave action had not yet had sufficient time nor vigor to effect a separation and transportation in the more distant portions of the beach. A well-defined selectivity was found at SW. Trout where the proportion of gravel and coarse sand decreased sharply from 36.5% at the 0 cm. station to 4.7% at the 80 cm. station and less than 1% at the 120, 160, and 200 cm. stations.

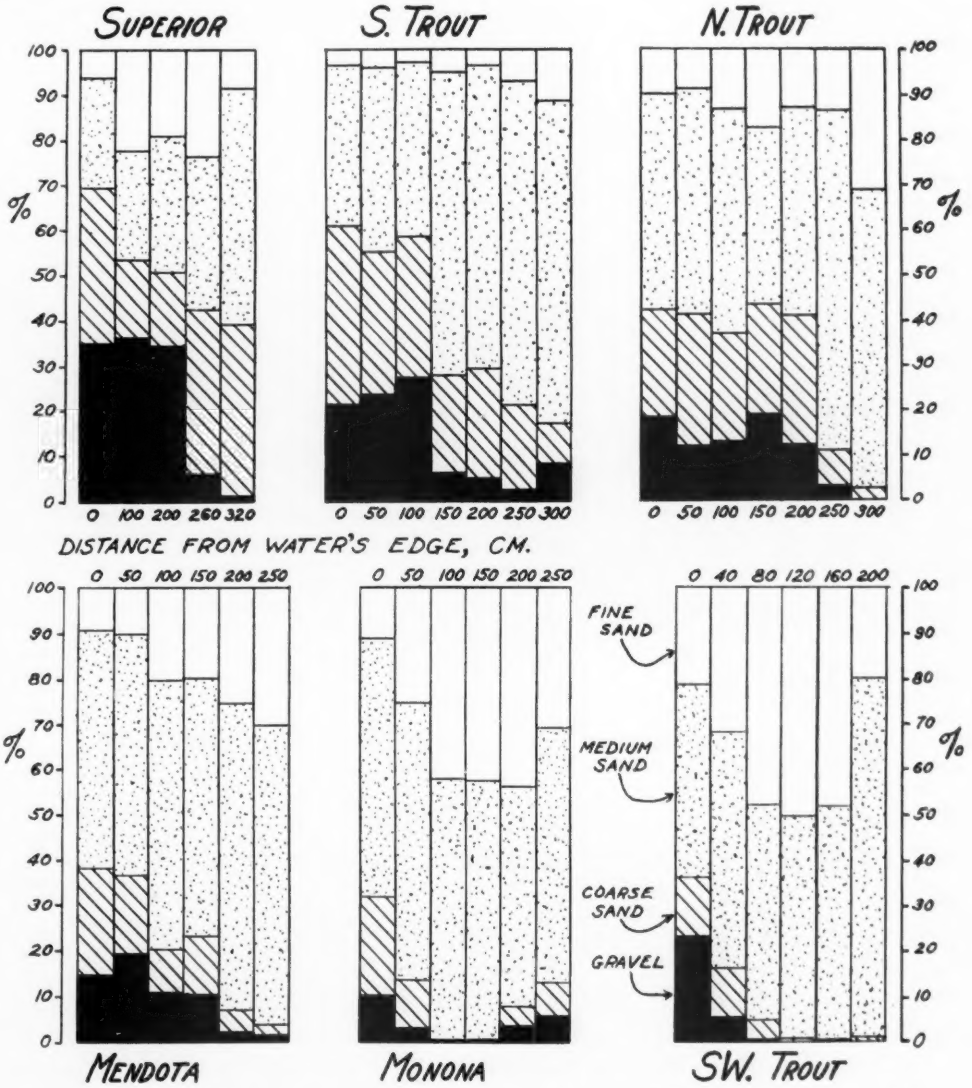


FIG. 7. Six beaches showing wave action selectivity. Composition of sand is given as relative weight percentages of gravel, coarse, medium, and fine sands. Distances from water's edge are given in cm.

In these six beaches the proportion of medium sand varied from 24% at the 0 and 100 cm. stations at Superior to more than 70% in the outer stations of the three beaches on Trout Lake. In most instances more than 50% of the sand was medium grade. S. Trout had the smallest proportion of fine

sand, with 11.1% at the 300 cm. station and less than 7.0% at all of the other stations. N. Trout and Mendota showed increasing amounts of fine sand at the outer stations. Superior, Monona, and SW. Trout, on the other hand, showed minimum amounts of fine sand both at the water's edge and at the outer edges of the beaches, with greater proportions between (up to 23.5%, 43.8%, and 50.5%, respectively). Although no measurements are available, the distribution of the grades at Michigan is comparable with that of Superior.

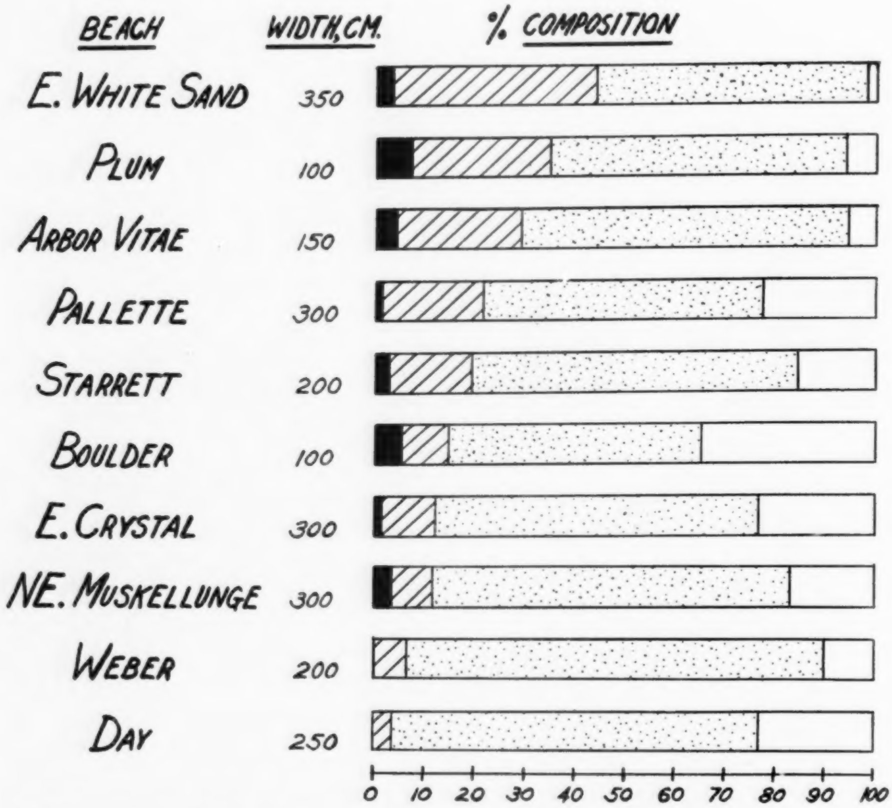


FIG. 8. Composition of ten beaches which show no selectivity. Solid black = gravel, diagonal hatching = coarse sand, stippled = medium sand, plain = fine sand.

At the other 13 beaches little sorting action was apparent, perhaps due to low percentages of gravel and coarse sand. The composition of large sand samples taken over the entire widths of 10 of these beaches are given in Figure 8. The greatest proportion of gravel was only 6.9% at Plum; Boulder was second highest with 5.7%. Day had no gravel, Weber had 0.1%, and Pallette 1.3%. Well-graduated variations in the amounts of coarse sand were found. E. White Sand had the most with 40.6% and Day the least with 3.7%. All of these beaches were composed of more than 50% medium sand, from 50.9% at Boulder to 83.4% at Weber. The amounts of fine sand varied

unevenly, having no relation to the amounts of the other grades. E. White Sand had the least with 1.9% and Boulder the most with 34.6%.

Although no data are available, NE. White Sand is similar to E. White Sand, E. Muskellunge is similar to NE. Muskellunge, and W. Crystal is similar to E. Crystal.

Throughout the course of this work it was noted that the grain of the sand may vary markedly in different places on the shores of hard-water lakes, but at soft-water lakes most beaches are of similar grain consistency.

Grade and Pore Space

So far as conditions of life in beaches are concerned, the sand particles are of no value in themselves. Nevertheless, they influence the quantity of capillary water in the sand as well as the magnitude of the spaces in which the organisms move about. Bruce (1928) states that a system of equal spheres in the closest possible contact has an aggregate volume of 74.04% of the space occupied and the spaces between the spheres will amount to 25.96%. In beaches, however, this relation never exists since the sand particles are not of the same size, nor are they spherical.

In order to ascertain the ratio for sand as it exists in beaches, approximations were carried out in the laboratory after the method of Bruce. Thirteen determinations were made, eight of them on grades of sand separated out by Tyler sieves, and one on the "raw" sand representative of the entire widths of each of Superior, S. Trout, E. White Sand, Starrett, and Day beaches. In all cases 60 cc. of water was added to 50 cc. of well-packed sand in a graduated cylinder and the two were thoroughly mixed. After allowing the sand to settle out, the graduate was jarred several times to pack the particles solidly, and the supernatant water was poured off into another cylinder, allowing one-half minute for drainage. The difference between this water and the original 60 cc. indicated the volume of the interstitial water retained by the sand. These rough measurements are summarized in Table 3. With one exception, the interstitial volume of the various types of sand varied from 37 to 43% of the aggregate volume. The low of 18% for gravel retained by the #12 sieve is due to the fact that the interstices between these grains are so large that there is little capillarity and consequently much of the water runs out from the spaces between the particles during the draining process. The mean of 42% for the seven uniform grades of sand as compared with 39% for the beach sands may be of some significance. This difference may be ascribed to the fact that in heterogeneous sands the smaller particles fill up some of the spaces between the larger particles which would otherwise be occupied by water (or air). In reality, then, in a beach sand there is slightly less interstitial space than in sand of uniform grade.

The inconsistency between 25.96% pore space in a system of equal spheres and 37% to 43% in the various sand samples may be explained on

TABLE 3. INTERSTITIAL SPACE IN VARIOUS SANDS

Sand	Percent interstitial space	Mean
Retained by sieve No. 12	(18)	
16	43	
20	42	
30	41	
40	43	42%
50	41	
70	42	
Passing sieve No. 70	41	
Superior	41	
S. Trout	38	
E. White Sand	37	39%
Starrett	38	
Day	40	

the basis of the uneven shape of sand grains which prevents a compact arrangement.

The outstanding fact concerning the present series of measurements is the small variation in interstitial volume in widely differing sands. Applying this fact to conditions in beaches, the pore space may be said to be practically uniform (about 40%) no matter whether the sand in the beach be fine or coarse, heterogeneous or homogeneous.

Wiszniewski (1934a) found that the interstitial water occupies 42% of the gross volume of the saturated sand. Sassuchin, Kabanov, and Neiswestnova (1927) give 37%. Both of these figures are based on only one determination. Bruce (1928) states that the interstitial volume varies directly according to the size of the sand particles, from 39% for sand grains .28 to .53 mm. in diameter to 44.7% for particles .09 to .11 mm. in diameter. He gives 20% as the interstitial volume of ungraded marine beach sand.

CAPILLARY WATER

The psammolittoral organisms are subject to two opposing currents of interstitial water; one is a slow, almost continuous upward current caused by the capillary water being drawn up through the sand because of evaporation at the surface; the other is a comparatively strong, intermittent, downward current caused by rains and wave action. Contrasted with other sources, rain contributes relatively little water to the beach near the water's edge. It is a very important factor, however, in the outer portions of beaches which are not exposed to the effects of waves and capillary rise of ground waters. When waves wash upon a shore a large portion of the water rushes back with their recession; another portion sinks immediately into the sand to the lake level; a third portion remains in the upper regions of the sand for a varying length of time. Upon cessation of wave action evaporation begins to get the upper hand and the sand begins to dry out, particularly in the outer stations. Although the capillary water at the 0 and 50 cm. stations of most

beaches is being renewed almost continually by the waves, thickly populated areas in the outer portions of many beaches were found over which the waves never wash.

Table 4 shows the mean values for 18 series of determinations made on the amount of water held in 12 beaches. In order to reduce errors to a minimum, samples on which weighings were made were taken at least 24 hours after rains and when there was little wave action or had not been for at least 12 hours. At the 0 cm. station there is no vertical gradient due to the immediate proximity of the lake maintaining complete saturation. At the 50 cm. station there is a poorly defined gradient, the lowest 5 cm. being practically saturated; the top 3 cm. show some evidence of drying with 86% saturation in the uppermost cm. Although the lowest 3 cm. at the 100 cm. station are almost completely saturated, a gradient is evident with 81% in the surface of the sand and 94% at a depth of 8 cm. All of the more distant stations showed clear cases of vertical gradients. The greatest difference between the top and bottom cm. of sand was found at the 200 cm. station where the

TABLE 4. MEAN PERCENTAGE OF SATURATION IN SANDY BEACHES

Depth, cm.	Distance from water's edge, cm.							
	0	50	100	150	200	250	300	350
1	100	86	81	68	41	34	20	—
2	99	94	84	74	45	38	25	3
3	101	96	87	78	52	40	29	6
4	100	100	89	81	61	44	32	7
5	100	98	90	86	64	49	32	8
6	98	98	93	88	66	52	39	10
7	100	100	96	90	69	54	40	18
8	99	99	94	91	74	57	42	23

saturation increased from 41% in the former to 74% in the latter. At the 350 cm. station the mean for the top cm. of sand was less than 1% and the bottom cm. reached 23% saturation. At the surface of the sand 81, 41, and 20% saturation were found for the 100, 200, and 300 cm. stations, respectively. At a depth of 3 cm. the corresponding amounts were 87, 52, and 29% saturation. Very few organisms were found in sand samples which had a saturation of less than 10%.

These figures vary considerably from time to time and from beach to beach, depending on slope of shore, amount of wind, sunshine, temperature, rains, and wave action. The least variable and most reliable of these factors in determining the distribution of the capillary water is slope.

To decide on the relation between size of sand grains, height above water level, and water content of sand, experiments were conducted on the rate and extent of capillary rise in various sands. Fourteen measurements were made, eight of them on uniform grades separated out by Tyler sieves and six on the ungraded beach sands taken over the entire width of the beaches. The

sand was placed in glass tubes having an internal cross-sectional area of approximately 2 sq. cm. The lower end of each tube was covered over with cheesecloth and placed in water and the rise of capillary water above the level of the source could be easily measured at intervals.

From Table 5 in which these measurements are shown, it will be seen that in homogeneous sands the amount of capillary rise is directly dependent upon the size of the grains, or rather the size of the capillary spaces between the grains. Within 10 minutes after the beginning of the experiments the water rose from 49 to 91% as high as it did during the ensuing 24 hours. At the end of that period the water was found to have risen only 8 mm. through gravel retained by the #12 sieve, while the fine sand which passed #70 sieve resulted in a capillary rise of 150 mm. Between these extremes

TABLE 5. RISE OF CAPILLARY WATER IN VARIOUS SANDS

Sand	Height (mm.) of water column	
	After 10 minutes	After 24 hours
Retained by sieve No. 12	7	8
16	12	13
20	17	20
30	21	40
40	32	52
50	40	60
70	63	96
Passing No. 70 sieve	80	150
N. Trout	38	63
Superior	41	67
E. White Sand	40	70
E. Crystal	43	70
S. Trout	42	78
Starrett	47	88

regular gradations in the height of the water column were found, depending on the particular sand used. Ungraded beach sands, however, showed no such wide range. The capillary water in N. Trout sand (which is relatively coarse) reached 63 mm., the lowest figure recorded, but in Starrett sand (relatively fine) the water reached 88 mm. Nevertheless, the measurements do not demonstrate a direct relationship. For example, both E. White Sand and E. Crystal sands showed the same capillary rise in spite of the fact that the former is appreciably more coarse, according to the method of measurement employed.

Compared with the graded sands, the water rose higher in the beach sands than would be expected. All of the ungraded beach sands showed a greater capillary rise than the medium sand retained by #50 sieve. This simply demonstrates that in beaches the spaces between the larger grains are filled with finer particles resulting in smaller capillary spaces than would be found in sand having a homogeneous composition.

These measurements account for the large degree of saturation in the 150 cm. of sand adjacent to the water's edge. In the drier outer regions rains and high waves play an increasingly important role by filling in the dry interstices and producing a broader inhabitable zone of sand than would be possible through the agency of capillarity alone.

The rate of evaporation of capillary water from the surface of the sand is of great importance from the standpoint of the organisms because of the cooling action on the sand. Nevertheless, in a series of rough determinations in the laboratory with various types of sand it was found that the size of the grains has little effect on the rate of evaporation, it being practically the same for coarse and fine sand.

TEMPERATURES OF SANDY BEACHES

There are a number of variable influences which may affect the temperature of the sand. These are lake water temperature, air temperature, amount of capillary water in the sand and its evaporation, wind, rain, and sunshine. The combined relative intensities of these factors determine the temperatures.

It has already been mentioned that temperatures of the sand were often taken by thrusting thermometers into the beaches at various stations. The height of the mercury column was read by holding a mirror at an angle of 45° so that the temperature could be recorded without removing the instrument from the sand. All temperatures were taken as being at the center of each successive cm. of sand at depths of 1, 2, 4, 6, and 8 cm. When a temperature was taken at the 4 cm. level, for example, the center of the thermometer bulb was actually 35 mm. below the surface. Table 6 shows a summary of eight series of temperature readings.

The temperature of the surface of the sand between the 50 and 250 cm. stations was found to be comparatively homogeneous due to the predominating influence of the capillary water. Differences of more than 2.5° between any two such points were seldom found. Beyond those limits, however, greater ranges in temperature were the rule. Near the water's edge the lake water serves to keep the sand temperatures near that of the lake and beyond 250 cm. the surface of the sand customarily becomes drier and consequently the sun may raise the temperature to 35° or even 40°C. Nevertheless, no reading higher than 32.5°C. was ever made between the lake and the 250 cm. stations.

In spite of the fact that the sand at the 200 and 250 cm. stations, and beyond in some beaches, contains relatively small amounts of capillary water, these small amounts are sufficient to keep the temperature of the sand down to a degree tolerated by the organisms inhabiting the sand.

In general, the differences in temperature between the top and 8 cm. levels of the 250 cm. of sand adjacent to the lake are small, usually less than 4°. Greater differences were not uncommon when the sun was shining brightly, but at night and under cloudy conditions the two sets of tempera-

tures were quite similar with only occasional differences of more than 1°. For the most part, the differences between the top and 8 cm. levels were smallest at the 0 cm. stations, but even there, under a hot sun and with little wind, the surface may be 3° warmer than the lower depth.

At Mendota on October 8, 1936 an unusual condition was found. Except at the water's edge, the surface of the sand was cooler than the deeper layers by 1° to 2°. This was due to the fact that the temperatures were taken in the morning when the air temperature was falling and before the sun had begun to act upon the surface of the sand. The same was true to a lesser extent at this beach on May 14, 1937.

TABLE 6. SAND TEMPERATURES

Temperatures are given for the top cm. of sand and the eighth cm. from the surface. Differences between these two sets of readings are also shown. Lake water temperatures were taken about 50 cm. from the water's edge.

Beach and date, 1937	Air temp.	Water temp.	Depth, cm.	Distance from water's edge, cm. 0	50	100	150	200	250	300	350
Monona			1	10.0	8.6	9.8	9.1	9.0	9.6		
October 29	12.8	9.0	8	8.4	7.7	7.5	7.1	7.0	7.0		
(sunny)				1.6	0.9	2.3	2.0	2.0	2.6		
Mendota			1	9.6	9.0	7.0	7.0	6.8	6.5		
May 14	4.5	9.8	8	9.2	9.0	7.0	7.0	7.0	6.8		
(8 A. M.)				0.4	0.0	0.0	0.0	—0.2	—0.3		
Mendota			1	11.0	7.0	6.0	5.4	5.1	5.0	5.5	
October 8	4.3	11.0	8	11.0	8.4	7.0	6.8	6.9	6.9	6.8	
(8 A. M.)				0.0	—1.4	—1.0	—1.4	—1.8	—1.9	—1.3	
NE. Muskellunge			1	20.0	16.0	15.0	15.1	15.0	15.4		
August 22	13.4	20.0	8	19.0	14.9	14.6	15.0	14.6	14.9		
(cloudy)				1.0	1.1	0.4	0.1	0.4	0.5		
E. White Sand			1	26.5	28.5	28.8	29.0	28.0	28.0	31.1	41.1
July 18	24.0	26.0	8	26.0	25.2	25.0	24.0	25.2	24.8	24.6	26.2
(sunny)				0.5	3.3	3.8	5.0	2.8	3.2	6.5	14.9
S. Trout			1	29.0	31.0	30.5	29.7	29.5	29.9	28.8	
August 15	29.0	27.1	8	26.0	27.0	26.5	25.1	26.1	25.4	25.0	
(sunny)				3.0	4.0	4.0	4.6	3.4	4.5	3.8	
N. Trout			1	27.9	32.0	31.9	31.1	31.2	31.0		
August 17	27.8	27.7	8	26.4	28.0	27.8	27.4	27.1	26.0		
(sunny)				1.5	4.0	4.1	3.7	4.1	5.0		
Pallette			1	29.7	29.1	30.6	29.5	29.3	30.5		
July 11	23.0	29.1	8	26.5	27.0	26.9	26.5	26.2	26.9		
(sunny)				3.2	2.1	3.7	3.0	3.1	3.6		

On August 8, 1937 four series of temperatures were taken at N. Trout at 8 A.M., 11 A.M., 4 P.M., and 7:30 P.M. in order to establish the daily course of temperatures at the different stations. The day was warm and although there were a few light clouds, sunny conditions prevailed. These temperatures, in Table 7, show several significant facts which are of importance in the life of the psammolittoral organisms. First, during a typical

summer day the temperature of certain areas in the sand may vary as much as 9°. This range was found in the top cm. of sand at the 150 cm. station. At the same station the temperature at the 8 cm. level ranged from 16.0° to 23.0°. On many days the range is undoubtedly greater. Second, as would be expected, the surface layers of sand, where most of the organisms are found, heat up and cool off much more rapidly than the deeper sand. This is shown by the negative differences in temperature in the readings taken at 7:30 P.M. The condition of higher temperatures in the deeper portions may persist through the cool of the night until the morning sun again warms up the surface. Third, in spite of the sunshine, the highest temperature recorded was only 26.0°C. at the surface of the 100 cm. station at 4 P.M. Fourth, the greatest temperature difference between surface and a depth of 8 cm. was 4.3° at the 250 cm. station at 11 A.M.

TABLE 7. DAILY COURSE OF SAND TEMPERATURES AT N. TROUT ON AUGUST 8, 1937
Temperatures are given for the top cm. of sand and the eighth cm. from the surface. Differences between these two sets of readings are also shown. Lake water temperatures were taken about 50 cm. from the water's edge.

Station	Depth, cm.	TIME			
		8 A. M.	11 A.M.	4 P. M.	7:30 P.M.
0 cm.	1	20.2	23.8	24.0	22.1
	8	19.2	21.5	22.5	21.9
		1.0	2.3	1.5	0.2
50 cm.	1	16.6	23.9	24.0	21.5
	8	16.5	23.8	24.0	22.1
		0.1	0.1	0.0	—0.6
100 cm.	1	16.3	25.0	26.0	21.9
	8	16.6	22.0	24.0	22.2
		—0.3	3.0	2.0	—0.3
150 cm.	1	16.0	24.0	25.0	21.0
	8	16.0	20.9	23.0	21.5
		0.0	3.1	2.0	—0.5
200 cm.	1	15.9	24.9	24.8	20.5
	8	16.0	20.8	22.1	21.0
		—0.1	4.1	2.7	—0.5
250 cm.	1	16.3	25.0	25.0	20.7
	8	16.2	20.7	22.0	21.0
		0.1	4.3	3.0	—0.3
300 cm.	1	16.0	24.1	25.0	20.9
	8	15.9	20.4	22.5	21.2
		0.1	3.7	2.5	—0.3
Air		18.0	24.0	25.1	23.6
Water		20.3	23.8	24.0	22.1

Wiszniewski (1934a) has made observations on the surface temperatures of the beach at Lake Wigry, Poland, and has found much the same conditions as the present writer. He ascribes the temperatures of the sand as being governed mainly by two factors: (1) insolation by the sun, and (2) the

cooling action brought about by the evaporation of the capillary water from the surface of the sand. The temperature of the air is regarded as being of little importance.

PARTICULATE ORGANIC MATTER

There are two general types of dead particulate organic matter in beach sands; one is a finely divided debris, present to some extent in all parts of all beaches; the other, less generally distributed, consists of larger particles such as bits of leaves, twigs, aquatic vegetation, and insect remains. This material is derived from several sources. Much of it originates landwards from the beach as dead vegetation and humus, either windblown or washed into the beach by rain. Another source is the lake itself; waves, winds, and currents serve to lodge much detritus on the beach. Except in the early spring, recognizable remains of plankton organisms which inhabit the open

TABLE 8. MILLIGRAMS OF PARTICULATE ORGANIC MATTER IN EIGHT BEACHES

Each value represents the mean loss on ignition for a vertical series of eight 10 cc. sand samples between the surface and a depth of 8 cm. Asterisk signifies the presence of a windrow of material, usually deposited on shore by wave action.

Beach	Date	Distance from water's edge, cm.							
		—50	0	50	100	150	200	250	300
Monona	June 28, 1937	1.8	1.0	8.3	9.4	5.8	19.4	....	....
	Sept. 8, 1937	....	5.5	1.6	10.0	9.4	13.4	8.9	....
	Oct. 29, 1937	....	.9	5.6	1.5	3.4	4.4	6.0	....
Plum	Aug. 19, 1938	2.0	3.3	5.2	46.7	....	....	....	....
N. Trout	July 4, 1937	.8	.6	2.3	1.5	.6	1.8	.7	.8
	July 18, 1937	....	.4	.3	.3	.6	.9	.8	.7
	Aug. 1, 1937	....	.9	.6	1.8	6.1	.7	5.2	.8
	Aug. 17, 1937	....	.7	.6	.8	.7	1.3	1.1	1.2
	July 3, 1938	....	.2	1.7	4.1	8.6	.5	....	....
	July 31, 1938	....	8.4	14.4*	36.3*	2.9	28.3	....	....
	Aug. 4, 1938	.5	2.4	7.6	2.3	8.7	5.3	....	....
	Aug. 26, 1938	3.4	1.1	1.1	128.7*	3.0	2.7	1.3	....
S. Trout	July 5, 1937	....	1.9	2.4	.6	7.4	6.1	13.1	....
	Aug. 15, 1937	....	2.1	6.8	3.7	1.5	1.1	1.4	....
	July 12, 1938	4.6	7.7	3.8	.7	2.2	....	....	....
	Aug. 15, 1938	3.8	5.9	9.3	59.9*	36.1*	....	....	....
Superior	Aug. 8, 1937	....	.3	....	.4	....	.6	.6	.7
	July 17, 1938	.3	.3	.5	.5	.2	.2	.2	....
E. White Sand	July 18, 1937	....	.5	.8	.7	11.0	2.1	25.7	1.1
	July 24, 1938	....	1.6	1.2	1.1	1.5	1.3	3.8	4.1
Starrett	July 30, 1937	....	6.0	.9	1.0	.7	7.3	....	....
	Aug. 7, 1938	3.8	3.0	8.7	15.3	53.4	44.1	....	....
E. Crystal	July 8, 1937	....	.4	.5	.6	2.4	1.1	1.9	2.2
	July 3, 1938	.2	.4	.7	.4	.8	1.0	1.5	....

waters of the lakes (Cyclops, Diaptomus, Keratella, Polyarthra, etc.) were present in negligible quantities in the sand and cannot be regarded as being of any significance in adding organic material to the sand. A third small source is the beach itself where the dead psammolittoral plants and animals contribute appreciably toward the particulate material.

During 1937 and 1938, 41 series of determinations were made of the particulate organic matter in 17 beaches. Some of the typical results are given in Table 8. One of the most striking facts gained from these and other

data is that there are relatively small amounts of particulate organic matter in the beaches studied. Very few individual 10 cc. sand samples contained more than 50 mg. and the great majority contained less than 5 mg.

The eight series of determinations at N. Trout demonstrate well what great variations in organic content may be found in a single beach over a period of time. At the 50 cm. station the range was 0.3 to 14.4 mg. per sample, and at the 100 cm. station, 0.3 to 128.7 mg. Comparable variations are shown for Starrett, S. Trout, and E. White Sand.

An important agency which serves to increase the amount of organic material is the deposition of large amounts of debris, often as visible windrows, 50 to 200 cm. from the water's edge. These windrows are shown in several cases for N. Trout and S. Trout in the table. The appearance of windrows and large deposits at the more unproductive, soft-water lakes was exceptional. Continual accumulation of organic material is prevented by bacterial decomposition and onshore winds which serve to blow some of the exposed dry debris away from the beach.

Very small amounts of organic material were found at E. Crystal and Superior. Only two stations at the former beach on July 8, 1937 had more than 2.0 mg. per sample. At Superior, in two series of determinations, only the samples at the 300 cm. station contained as high as 0.7 mg. per sample.

At most beaches, the exposed sand within 50 cm. of the water's edge is kept washed quite clean. The larger amounts of organic material are nearly always characteristic of the outer portions of the sand. With respect to the organic material in the submerged sand within 50 cm. of the water's edge, the amounts were comparable with those found in the sand at the 0 cm. stations. Vertically, the largest quantities of debris were usually found in the uppermost 3 cm. of sand, but exceptional and sporadic distributions were numerous.

DIVERSITY OF PHYSICAL CONDITIONS

Table 9 emphasizes the variety of physical conditions occurring in the beaches investigated. In hardness of lake water, Monona and Mendota are highest with 75 to 80 ppm. of bound carbon dioxide; Trout is intermediate with 19.0 ppm.; Starrett, Day, Crystal, and Weber are all low with between 1.0 and 2.0 ppm. As to exposure to wave action, the beach at Lake Superior is in a class by itself, being subject to continuous heavy wave action. Of the other beaches, N. Trout and NE. Muskellunge are next in order with strong, although intermittent waves which may reach as far as 3 m. from the shoreline. At the other extreme, Day, Boulder, and Plum beaches have practically no wave action. The composition of the beaches ranged from a distinct gravelly condition at Michigan, Superior, and S. Trout to a preponderance of medium and fine sands at Day, Weber, and SW. Trout. Mean organic material ranged from 0.4 and 0.6 mg. per 10 cc. of sand at Superior and Michigan, respectively, to 6.7 at Monona and 11.5 mg. at Starrett. The

results for Arbor Vitae, W. Crystal, and Weber are only approximations, since few actual measurements were available for these beaches.

Except for the fact that the beaches of the soft-water lakes are composed of fine sand, there seem to be no significant correlations between exposure, sand grain size, particulate organic material, and hardness of lake waters.

TABLE 9. SUMMARY OF SOME PHYSICAL CONDITIONS IN THE 20 BEACHES STUDIED
Under hardness of lake waters 1 = hardest and 15 = softest; under exposure to wave action 1 = most exposed and 20 = least exposed; under sand grain size 1 = coarsest sand and 20 = finest sand; organic material given as mean quantity per 10 cc. sand sample in that portion of the beach inhabited by psammolittoral organisms.

Beach	Hardness of lake water	Exposure to wave action	Sand grain size	Organic material. mg./10cc. of sand
Monona	1	10	16	6.7
Mendota	2	5	5	5.5
Arbor Vitae	3	9	9	4.0 (?)
Plum	4	20	8	4.3
N. Trout	5	2	4	5.6
S. Trout	5	8	3	7.5
SW. Trout	5	17	18	2.7
Michigan	6	4	2	0.6
Superior	7	1	1	0.4
E. White Sand	8	7	7	4.1
NE. White Sand	8	6	6	3.1
Boulder	9	19	12	4.6
NE. Muskellunge	10	3	17	1.1
E. Muskellunge	10	12	13	4.1
Pallette	11	16	10	2.6
Starrett	12	13	11	11.5
W. Crystal	13	15	14	1.6 (?)
E. Crystal	13	11	15	1.0
Day	14	18	20	4.5
Weber	15	14	19	2.0 (?)

CHEMISTRY OF THE CAPILLARY WATER

HYDROGEN ION CONCENTRATION

During 1937, pH determinations were made on the capillary waters of 13 beaches, and, for comparison, readings were usually also made on the lake water within 50 cm. of the water's edge. Table 10 shows the results obtained. At Monona (two series), Mendota (Oct. 15), and E. Crystal there was a variation of only .2 of a pH unit or less between the lake water and the capillary water at the 100 cm. stations. In the last of these cases all readings were the same, i.e., pH 8.1. In most instances greater variations were found. The most pronounced divergence occurred at N. Trout where the pH of the lake water was 8.1 and the capillary water at 100 cm. showed pH 6.8. SW. Trout, S. Trout, Weber, NE. Muskellunge, Mendota (Sept. 7) and E. White Sand all showed differences of .4 of a pH unit or more between lake water and certain capillary samples. It is significant that the more acid situations were usually 50 or 100 cm. from the water's edge. Although we

have no direct evidence, we believe that even lower pH values prevail at 150 and 200 cm. from the water's edge.

In general, however, there was a definite correlation between the pH of capillary water and the pH of the lake water at the same shore. That is, the alkaline lakes had alkaline capillary water in their beaches, and the acid lakes had acid capillary water in their beaches.

These results do not agree with most of those of Wiszniewski, who found (1934a, 1935a, 1936) that the pH of capillary water in a number of beaches was the same as that of the adjacent lake water, even though determinations

TABLE 10. pH OF LAKE AND CAPILLARY WATERS AT 13 BEACHES, 1937
(—25 cm. signifies lake water 25 cm. from the water's edge.)

Beach and date	Distance from water's edge, cm.				
	Lake water		Capillary water		
	Open water	—25	0	50	100
Monona.........Sept. 13.......	...	8.1	8.0	8.0	8.0
Monona.........Oct. 30.......	...	8.1	8.0	8.0	8.0
Mendota........Sept. 7.......	8.7	8.8	8.7	8.5	8.4
Mendota........Oct. 15.......	8.1	8.1	8.1	8.1	8.1
N. Trout........Aug. 26.......	7.6	8.1	7.1	7.0	6.8
S. Trout.........Aug. 15.......	...	8.2	...	7.2	7.3
SW. Trout.......Aug. 15.......	...	8.1	7.3	6.9	...
E. White Sand...Aug. 19.......	7.6	7.2	7.0	6.7	6.8
Boulder.........Aug. 14.......	7.5	...	7.0	6.9	...
NE. Muskellunge.Aug. 22.......	7.3	7.1	6.7	6.8	...
Pallette.........Aug. 14.......	6.7	...	...	6.5	6.5
Weber...........Aug. 28.......	6.3	6.3	6.1	5.8	...
Starrett.........Aug. 22.......	6.4	6.4	6.4	6.2	...
Day............July 27.......	5.9	6.1	6.1	6.0	6.0
E. Crystal.......Aug. 28.......	6.2	6.1	5.9	5.8	5.9

were made as far back as 270 cm. from the water's edge. In a later study (1936b) he reported more acid conditions in the sand than in the lake water. Stangenberg, working at Lake Wigry, recorded the lake as being pH 7.3; the capillary water from two stations on the beaches (80 cm. from the water's edge) showed pH 7.0 and pH 7.2.

It is very likely that the pH of the capillary water at any point is subject to much greater changes than the open waters of lakes, depending on immediate physical, chemical, and biological conditions. Water content, wave action, organic material, evaporation, and bacterial action undoubtedly have pronounced effects. These relationships are yet to be determined.

CARBON DIOXIDE CONTENT

The outstanding characteristic of the carbon dioxide content of the capillary water, as shown in Table 11, was the great variation, both within the same series of samples, and also from beach to beach. The range of free carbon dioxide in the Vilas County beaches was from 2.0 ppm. at the 0 cm.

station at E. Crystal to 89.0 ppm., at the 50 cm. station at SW. Trout. In the Madison beaches the range was rather narrow, from 4.0 ppm. at the 0 cm. station at Mendota to 13.0 ppm. at the 100 cm. station on the same beach. These lower quantities may be due to the fact that the readings were made in the fall when biological activities in the sand were going on more slowly. Near shore the free carbon dioxide of the lake water varied from —3.0 to 4.0 ppm., the harder lakes having both extremes and the softer lakes having a range of only 0.5 to 1.0 ppm. Two samples of capillary water taken from the sand 50 cm. below the water line at Monona in the fall of 1937 showed high free carbon dioxide content, 7.5 and 16.5 ppm.

There is evidence that wave action indirectly governs the amount of free carbon dioxide in the capillary water. On the exposed locations low carbon dioxide may be due to two functions of the waves: (1) they bring into the sand a continuous supply of lake water which is low in free carbon dioxide, and (2) they serve to keep the inner beach washed clean, thereby preventing bacterial action, which is, no doubt, an important factor in the production of free carbon dioxide.

Landwards from the water's edge, a pronounced free carbon dioxide gradient was found in all beaches. At E. White Sand, for example, the lake water near the shore contained 4.0 ppm. free carbon dioxide; at the 0 cm. station the capillary water contained 6.0 ppm.; at 50 cm. the reading was 11.0; and at the 100 cm. station it was 38.0 ppm. Because no capillary samples could be easily taken beyond 100 cm., the amounts of free carbon dioxide in the more distant and drier portions of the sand are not known. Nevertheless, it seems logical to expect comparatively large quantities there.

Although the data show it to only a minor extent, the author believes that the amount of free carbon dioxide may vary widely in the beaches from time to time due to changing chemical, physical, and biological conditions.

Stangenberg gives the free carbon dioxide content of Lake Wigry as 0.0, but in two of the beaches it reached 6.2 and 41.0 ppm. at a distance of 80 cm. from the water's edge.

There are several sources of bound carbon dioxide (equivalent to the "fest gebundene" of Pia) in the capillary waters. Rainwater washing over the surface of the earth and running onto the sand probably brings in small quantities; lake water washing upon the shore brings carbonate to the sand; and third, the "ground water" which is drawn up from the deeper layers and evaporated at the surface leaves behind quantities of carbonate.

The distribution of bound carbon dioxide in the beaches is neither so regular nor as easily explained as is the case with the free carbon dioxide. In most instances there were greater quantities in the capillary water than in the lake water. Pronounced accumulations were found in the sand at E. White Sand and the three beaches at Trout Lake. At E. White Sand, for

example, the capillary water at the 100 cm. station contained 40.0 ppm. of bound carbon dioxide, compared with 16.0 ppm. for the lake water at the shore. At SW. Trout, 54.0 ppm. were found in the sand at the 50 cm. station, and only 19.0 ppm. in the lake water. The beaches of the softer lakes, such as Weber, Starrett, Day, and Crystal, also showed accumulations of bound carbon dioxide in the sand over the amount contained in the water adjacent to the shore. Of these lakes, however, the greatest amount found in the capillary water was only 4.0 ppm. at the 100 cm. stations of the last two mentioned. The lake water in these cases contained 1.0 ppm.

TABLE 11. BOUND AND FREE CO_2 IN CAPILLARY WATER OF 13 BEACHES, 1937
Expressed as parts per million.

Beach and date	Distance from water's edge, cm.									
	Lake water				Capillary water					
	Open water		—25		0		50		100	
	Free	Bound	Free	Bound	Free	Bound	Free	Bound	Free	Bound
Monona............Sept. 13	......	......	2.0	80.6	3.5	80.0	4.0	83.6	4.5	75.6
Monona............Oct. 30	......	......	4.0	82.6	9.5	84.6	10.5	87.0	11.0	89.0
Mendota...........Sept. 7	—4.0	75.0	—2.0	74.8	4.0	72.0	5.0	78.8	11.0	75.6
Mendota...........Oct. 15	......	......	4.0	86.0	9.9	83.6	12.0	86.0	13.0	87.6
N. Trout...........Aug. 26	1.0	19.6	—3.0	17.0	8.0	17.0	9.0	23.0	16.0	12.0
S. Trout............Aug. 15	......	......	3.0	23.0	......	......	16.0	30.5	19.0	33.0
SW. Trout..........Aug. 15	......	......	3.5	19.0	19.5	36.0	89.0	54.0	......	......
E. White Sand......Aug. 19	1.4	17.7	4.0	16.0	6.0	15.0	11.0	11.5	38.0	40.0
Boulder............Aug. 14	2.4	13.0	......	......	9.0	18.0	31.0	23.0	......	......
NE. Muskellunge....Aug. 22	2.0	9.5	0.5	9.0	3.5	8.0	4.5	12.0	......	......
Pallette............Aug. 14	1.3	3.8	......	......	......	......	18.0	11.0	20.0	13.0
Weber.............Aug. 28	1.8	1.8	0.5	1.0	6.5	1.5	20.5	1.5	......	......
Starrett............Aug. 22	1.9	1.9	1.0	1.6	2.5	1.6	10.0	3.0	......	......
Day...............July 27	1.0	1.3	1.0	1.0	9.0	1.5	28.0	3.5	33.0	4.0
E. Crystal..........Aug. 28	1.0	1.4	1.0	1.0	2.0	1.0	16.0	2.0	22.0	4.0

The data for the Madison beaches show no well-defined instances of accumulation of bound carbonates in the sand. Although minor variations occurred, most of the capillary samples contained approximately the same quantities of bound carbon dioxide as the lake water. The lowest reading was 72.0 ppm. at the 0 cm. station at Mendota, and the highest was 89.0 ppm. at the 100 cm. station at Monona.

In several instances less bound carbon dioxide was found in the capillary samples than in the lake water. The 100 cm. station at N. Trout, the 50 cm. station at E. White Sand, and the 0 cm. station at NE. Muskellunge gave such results.

The data for the three beaches at Trout Lake indicate that a considerable range of conditions may be found in different beaches on the same lake. It may be inferred also that the amount of bound carbon dioxide in a particular beach may vary considerably over a period of time.

DISSOLVED OXYGEN

The outstanding characteristic of the dissolved oxygen distribution in the sand was the pronounced horizontal gradient. Comparatively high quantities were found at the water's edge and small amounts at the 100 cm. stations. In all cases the dissolved oxygen in the capillary water at the water's edge was lower than the amount in the lake water immediately adjacent (Table 12). In the sand, the lowest quantity at 0 cm. was 3.4 ppm. at both Monona (Sept. 13) and E. Crystal; the highest was 7.7 ppm. at Boulder. The range at the 50 cm. stations was from 0.1 ppm. at Day to 2.7 ppm. at Monona (Oct. 30). Farther from the water's edge the oxygen content was still

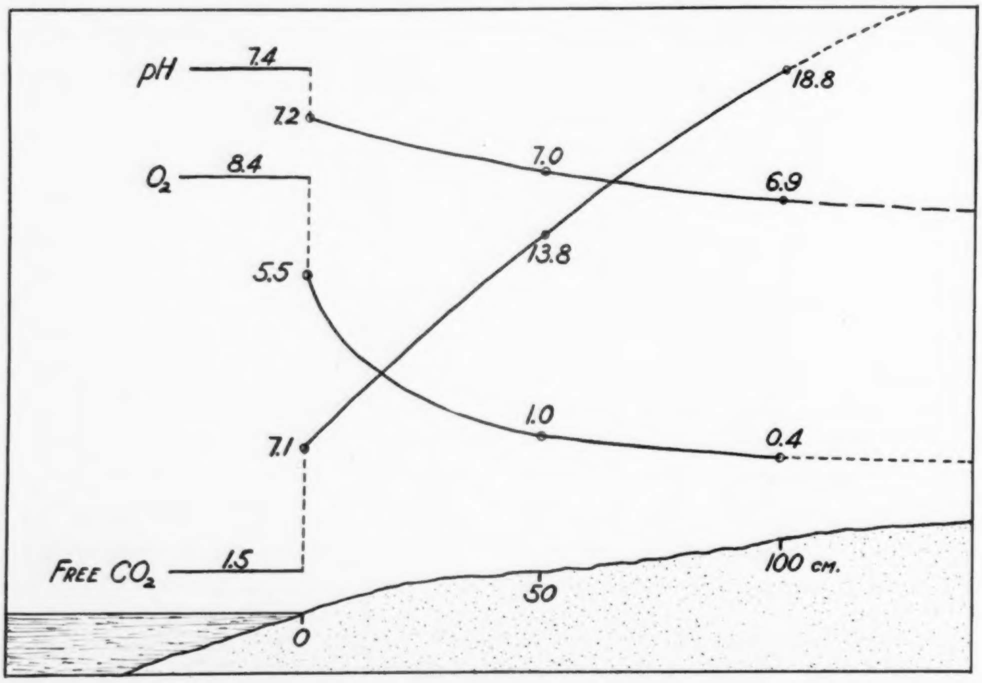


FIG. 9. Typical chemical characteristics of capillary water in an average beach. Values to the left of the 0 cm. station are for lake water. Curves beyond the 100 cm. station are theoretical. Oxygen and free carbon dioxide are indicated in parts per million. (After Pennak, 1939b).

lower; it varied from 0.0 at the 100 cm. station at Day to 0.8 ppm. at S. Trout. Mean quantities for 15 series of determinations give 8.4 ppm. for the lake water 25 cm. from the 0 cm. station, and 5.5, 1.0, and 0.4 ppm. at the 0, 50, and 100 cm. stations, respectively. In general, similar conditions were found in the Polish beaches by Wiszniewski.

Evidence of very low oxygen concentrations was found in the deeper samples at stations more distant than 100 cm., especially at Starrett and Day. In these beaches, beyond the 150 cm. stations, the sand showed distinct black, or dark-colored strata at depths of 6 to 10 cm. Such conditions have been noted by various workers on sea beaches (v. Bruce, 1928a). It has been well

established in these cases that the dark-colored layers are due to ferrous sulphide formation under anaerobic conditions in the presence of organic material. In the Wisconsin samples the odor of hydrogen sulphide could be detected in the sand upon exposure. On contact with air the color changed to brown or yellow.

Although the evidence is not adequately presented here, one of the most important factors in replenishing the oxygen supply in the sand is wave action, which renews the capillary water continuously in many beaches. Of the significance and degree of diffusion of the oxygen from the air into the sand, we know practically nothing, but presumably it is an important factor, especially in the middle beaches. It must be remembered that the water

TABLE 12. DISSOLVED O_2 IN LAKE AND CAPILLARY WATERS, PPM., 1937
(—25 signifies lake water 25 cm. from water's edge.)

Beach and date	Distance from water's edge, cm.				
	Lake water		Capillary water		
	Open water	—25	0	50	100
Monona.........Sept. 13.......	...	8.6	3.4	1.9	0.3
Monona.........Oct. 30.......	...	8.5	3.9	2.7	0.5
Mendota........Sept. 7.......	9.0	8.6	6.0	1.1	0.5
Mendota........Oct. 15.......	...	8.7	7.2	1.0	0.4
N. Trout........Aug. 26.......	8.8	9.5	4.6	0.6	0.5
S. Trout.........Aug. 15.......	...	8.5	...	0.7	0.8
SW. Trout.......Aug. 15.......	...	9.8	3.7	0.2	...
E. White Sand...Aug. 19.......	8.4	8.0	7.0	4.4	0.1
Boulder.........Aug. 14.......	6.8	...	7.7	0.3	...
NE. Muskellunge.Aug. 22	8.4	8.0	7.6	0.9	...
Pallette..........Aug. 14.......	8.2	...	...	0.3	0.4
Weber...........Aug. 28.......	8.5	7.8	5.1	0.6	...
Starrett.........Aug. 22.......	8.9	8.3	7.2	0.6	...
Day.............July 27.......	8.3	7.4	5.0	0.1	0.0
E. Crystal.......Aug. 28.......	8.5	7.9	3.4	0.6	0.2
Mean		8.4	5.5	1.0	0.4

samples on which oxygen determinations were made were taken at a depth of 4 cm., representing the midpoint of the vertical series of eight sand samples. More precise methods are necessary to determine the amounts present in the top cm. of the sand as contrasted with the samples at a depth of 8 cm. Wiszniewski states that "Si nous enfonçons notre pipète dans le sable, même à une profondeur de peu de cm, nous pouvons constater un changement assez considérable de la composition de l'eau retirée . . . tandis qu'en même temps la quantité d'oxygène qui y est dissout diminue notablement," but gives no data to support the statement.

ORGANIC AND INORGANIC RESIDUES

One of the fruitful sources of information concerning the dynamics of lake chemistry may lie in the study of the interchange of dissolved substances between lake waters and the capillary waters of the adjacent beaches. Aside

from this problem, however, determinations of the total residues of the capillary waters of 13 beaches were made in order to formulate a rough conception of the chemical nature of the environment of the psammolittoral organisms. These results are given in Table 13. Total residues for the open waters of the lakes were supplied from the records of the Wisconsin Geological and Natural History Survey.

Wherever data are available it was found that lake water taken 25 cm. from the shoreline contained greater total residues than the open waters of the lakes. The range was from 20% more at N. Trout and 40% more at Day to 350% at Weber and 435% at Starrett. In some instances these differences were due to accumulations of organic materials near shore and in other instances inorganic substances were obviously responsible.

Furthermore, the capillary water usually showed an accumulation of dissolved materials over the amount found in the lake water at the shore. The amounts in the lake water adjacent to the beaches ranged from 200 to 284 mg./l. at the Madison beaches, but at the Vilas County beaches the range was from 21 mg./l. at Day to 100 mg./l. at Starrett. The total residues of the capillary waters ranged between 48 mg./l. at the 100 cm. station at Day to 343 mg./l. at the corresponding station at Monona.

Although the total residues of the capillary water in the beaches of soft-water lakes were usually much lower than those from harder lake beaches, there were proportionately greater accumulations of dissolved materials in the former. The mean amount of dissolved material in the capillary waters of the Madison beaches was only 105% as much as the adjacent lake waters contained, but the soft-water beaches such as Weber, Day, Starrett, and E. Crystal contained from 122% to 420% as much. In general, the medium-hard beaches showed an intermediate condition. Six exceptions were found, where the capillary water samples contained from 90% to 99% as much total residue as the adjacent lake water. Three of these exceptions occurred at Mendota and Monona.

There was no indication of a residue gradient in the capillary waters. NE. Muskellunge, Starrett, and Day all had maxima at the 0 cm. stations; N. Trout had a maximum at the 50 cm. station: S. Trout, E. White Sand, Pallette, and E. Crystal all had maximum amounts of dissolved material at the 100 cm. station. If the total residue of the lake shore water be represented by 100%, the mean quantities in the sand will be 151, 160, and 151% at the 0, 50, and 100 cm. stations, respectively.

With respect to the inorganic fraction (ash) of the residues, the same general remarks apply as have just been made for the total residues: (1) A great variation was found, from 6 mg./l. at the 100 cm. station of Day to 224 mg./l. at the corresponding station at Monona. (2) The accumulations in soft-water lake beaches were proportionately greater than in other beaches. (3) Although much variation was found horizontally, especially in the soft-

TABLE 13. DISSOLVED ORGANIC AND INORGANIC MATERIALS IN CAPILLARY AND LAKE WATERS, 1937

Expressed as mg. per liter of water. Lake water 25 cm. from the water's edge indicated as —25.

Beach and date	Distance from water's edge, cm.	Total residue	Ash	Loss on ignition
Monona, September 13	—25	284	114	170
	0	306	118	188
	50	256	138	118
	100	343	224	119
Monona, October 30	—25	250	144	106
	0	291	203	88
	50	269	157	112
	100	269	180	89
Mendota, September 7	—25	200	100	100
	0	207	108	99
	50	220	117	103
	100	204	113	91
Mendota, October 15	—25	212	112	100
	0	221	125	96
	50	202	95	107
	100	210	113	97
N. Trout, August 26	open water	58	..	..
	—25	73	40	33
	0	86	46	40
	50	103	52	51
	100	80	46	34
S. Trout, August 15	—25	96	40	56
	50	120	51	69
	100	136	68	68
SW. Trout, August 15	—25	90	32	58
	0	103	34	69
	50	190	87	103
E. White Sand, August 19	open water	51	..	..
	—25	80	17	63
	0	75	20	55
	50	79	27	52
	100	139	64	75
Boulder, August 14	open water	59	..	..
	—25	99	35	64
	0	121	52	69
	50	129	43	86
NE. Muskellunge, August 22	open water	39	..	..
	—25	83	29	54
	0	104	48	56
	50	80	34	46
Pallette, August 14	open water	30	..	..
	—25	50	19	31
	50	57	10	47
	100	76	21	55
Weber, August 28	open water	12	..	..
	—25	42	16	26
	0	67	29	38
	50	176	88	68
Starrett, August 22	open water	23	..	..
	—25	100	69	31
	0	286	198	88
	50	122	65	57
Day, July 27	open water	15	..	..
	—25	21	6	15
	0	74	15	59
	50	59	10	49
	100	48	6	42
E. Crystal, August 28	open water	13	..	..
	—25	31	5	26
	0	51	29	22
	50	80	26	54
	100	86	54	32

water lake beaches, the mean for all samples showed about 54% more dissolved inorganic material in the sand than in the adjacent lake water.

The following remarks apply to the dissolved organic material in capillary waters. (1) The quantities found covered a smaller range than the inorganic materials; the smallest amount was 22 mg./l. at the 0 cm. station of E. Crystal and the greatest quantity was 188 mg./l. at the 0 cm. station at Monona. (2) In 26 out of 38 determinations the capillary water contained more organic material than the adjacent lake water. (3) As above, the softer lake beaches showed proportionately greater accumulations than the hard-water lake beaches. Mean amounts at Monona and Mendota were 5% less than the water near the shore contained but Weber, Starrett, Pallette, Day, and E. Crystal contained 50 to 200% more. (4) If the dissolved organic material in the lake water at the water's edge be represented by 100%, means for all determinations on the capillary water will be equivalent to 141, 152, and 127% at the 0, 50, and 100 cm. stations, respectively. (5) The proportion of organic material in the total residues ranged from 30% to 88%, with a mean for all samples of 54%.

The results obtained in this portion of the investigation are by no means conclusive, but merely serve to give a general idea of the relative concentrations of electrolytes and organic materials dissolved in the interstitial water. Undoubtedly, the amounts of these materials vary markedly from time to time. Some of the factors which aid in producing these variations may be wave action, evaporation, and lake productivity. Determinations on the capillary waters of such beaches as Superior and Michigan, where there is very little organic material, may serve to clear up some of these relationships.

These results agree with those found at Lake Wigry by Stangenberg who states that the total residues from several capillary samples contained from 114 to 194% as much material as the lake water.

PSAMMOLITTORAL ORGANISMS

Tardigrada

Tardigrada or "water bears" are also often called "moss animalcules" because of their frequent occurrence in moss. At first thought it seems contradictory to expect representatives of this group in sand since their food is commonly recognized as being juices sucked out of plant stems by means of the piercing stylet and sucking pharynx of these animals. Such food in beaches is exceptional. However, according to Marcus (1929) tardigrades also subsist on certain algae, particularly desmids and filamentous species, as well as occasional Nematoda, Rotatoria, and root hairs. Such foods are abundant in the sand and it is possible to see how this environment can support large populations, as some of the beaches do. Several hundred specimens were examined during the course of this study but all were found

to belong to the genus Macrobiotus (Schultze). Species were not determined because of difficulties brought about by improper fixation and lack of eggs.

GENERAL DISTRIBUTION

Table 14 gives a summary of the numbers of Tardigrada found in 13 beaches. Results for the other seven beaches, which contained very few or no tardigrades, are not shown. Nevertheless, certain of the total of 66 series of sand samples may be arbitrarily grouped together on the basis of horizontal and vertical distribution of these animals in the sand. In the first category may be placed 32 series of samples, each of which had a total of less than 10 specimens, usually scattered at random. Thirteen of these series contained no specimens at all, including Superior, Michigan, certain spring and fall samples at Monona and Mendota, NE. White Sand, E. Muskellunge and S. Trout in 1938. Table 15 shows the detailed distribution of tardigrades at N. Trout on Aug. 1, 1937 when only five specimens were found. A somewhat similar condition was found in certain Monona, Mendota, S. Trout, SW. Trout, E. White Sand, Boulder, and E. Crystal collections during 1936-1938.

In the second group may be placed those series of samples showing a total of 10 to 40 tardigrades scattered throughout the samples. Mendota, on May 18, 1936, showed such a population with 21 specimens in the samples taken between the 60 and 210 cm. stations; only one sample contained as many as three specimens. Similar populations were found at Mendota during the fall of 1937, Arbor Vitae, N. Trout (two series), S. Trout on Aug. 13, 1936, and at Day on Aug. 2, 1936.

The third group comprises collections containing between 40 and 200 tardigrades distributed in a sporadic manner in the beaches. Pallette, on July 11, 1937 demonstrated this condition with a total of 88 specimens; except for 27 at a depth of 3 cm. at the 150 cm. station and 22 at the same depth at the 250 cm. station, comparatively small numbers were found in the samples; none were found in the top cm. of any of the seven stations between 0 and 300 cm., a very unusual condition. Comparable distributions were found at Mendota during the late spring of 1937, Pallette in 1937, Boulder in 1938, and E. Crystal during 1937 and 1938 (one series in each year).

In the fourth group may be placed those series of samples which showed a concentration of tardigrades near the water's edge. The narrow beach at Plum Lake exhibited this condition markedly. On July 22, 1936 (see Table 15) 224 specimens were found in the samples taken at the 25 cm. station. The maximum number in any one sample was 75, at a depth of 4 cm. In contrast, the samples at the 0, 50, 75, and 100 cm. stations contained totals of only four, 37, three, and one specimens, respectively. Large concentrations within such narrow limits were found only at Plum. Less pronounced concentrations within 50 cm. of the water's edge were found at NE. Muskel-

TABLE 14. SUMMARY OF DISTRIBUTION OF TARDIGRADA IN 13 BEACHES

Distance from water's edge indicated horizontally in cm. Each value represents the total number of organisms found in the eight successive 10 cc. sand samples, each one cm. in thickness, between the surface of the sand and a depth of 8 cm. Results have been interpolated in some instances where stations were not established at 50 cm. intervals. Very few tardigrades were found in the seven beaches not indicated in this table; see text for details.

Beach	Date	Distance from water's edge, cm.								
		—50	0	50	100	150	200	250	300	350
Mendota	May 18, 1936	...	3	1	3	8	3	0	...	...
	Sept. 1, "	...	0	4	10	13	119	...	...	...
	Nov. 12, "	...	0	0	0	0	0	...	...	...
	Apr. 16, 1937	...	0	0	0	0	0	0	...	...
	May 7, "	...	0	0	0	0	0	...	...	...
	May 14, "	...	1	0	0	0	0	0	...	...
	May 28, "	...	5	15	6	46	14	1	...	...
	June 4, "	...	7	48	6	1	8	3	...	...
	June 22, "	0	0	0	3	126	23	17	...	...
	Sept. 3, "	...	21	0	8	1	0	0	...	...
	Oct. 8, "	...	0	0	2	1	10	8	0	...
Arbor Vitae	Aug. 8, 1936	...	0	3	2	3	...	...	...	...
Plum	July 22, 1936	...	4	37	1	...	...	...	...	...
	Aug. 19, 1938	3	73	4	0	...	...	...	...	...
N. Trout	July 5, 1936	...	0	2	9	2	...	...	...	...
	Aug. 16, "	...	0	1	2	0	0	0	...	...
	July 4, 1937	0	0	1	2	1	5	3	56	...
	July 18, "	...	0	0	0	0	0	0	13	...
	Aug. 1, "	...	1	0	0	0	0	0	3	1
	Aug. 17, "	...	0	0	5	1	0	0	12	3
	July 3, 1938	...	0	0	2	0	0	...	...	...
	July 31, "	...	0	3	0	0	0	...	...	...
	Aug. 4, "	0	0	0	0	0	4	...	...	...
	Aug. 26, "	0	0	0	2	0	0	0	...	...
SW. Trout	July 19, 1936	...	0	5	0	...	...	...	...	...
	Aug. 13, "	...	0	0	1	...	...	...	...	...
	July 23, 1937	...	33	6	78	65	14	...	...	...
Boulder	Aug. 2, 1936	...	7	82	2	...	...	...	...	...
	Aug. 14, 1937	...	0	3	...	...	...	...	...	...
	July 24, 1938	8	9	0	38	7	...	...	...	...
NE. Muskellunge	July 16, 1936	0	3	67	2	0	...	...	...	...
	Aug. 21, "	...	92	147	354	314	56	2	...	...
	July 13, 1937	...	51	23	1	0	...	...	...	...
	Aug. 22, "	...	13	259	200	16	0	0	0	...
Pallette	July 30, 1936	...	29	115	131	96	12	...	...	...
	July 11, 1937	...	4	0	2	41	4	31	6	...
	July 10, 1938	11	10	9	12	36	105	...	...	...
Weber	July 29, 1936	...	0	1	0	...	...	...	...	...
	Aug. 11, "	...	3	18	3	20	2	...	...	...
Starrett	July 30, 1937	...	3	83	68	31	177	...	...	...
	Aug. 7, 1938	22	65	0	0	0	0	...	...	...
Day	Aug. 2, 1936	...	6	1	0	...	...	...	...	...
	July 27, 1937	...	9	657	375	250	13	2	...	...
W. Crystal	July 9, 1936	...	21	3	...	...	...	...	...	...
E. Crystal	July 9, 1936	...	0	10	146	184	27	...	...	...
	July 8, 1937	...	41	0	0	3	36	6	0	...
	July 3, 1938	0	0	0	59	6	38	0	...	...
	Aug. 23, "	2	1	0	0	0	0	0	...	...

lunge, Starrett, and W. Crystal. Of these four beaches, W. Crystal and Plum are narrow, but the other two are comparatively broad.

In the fifth group may be included those series of samples which showed concentrations of Tardigrada in the outer regions of the beaches. N. Trout on July 4, 1937 (Table 15) showed this condition, with a total of 56 speci-

TABLE 15. DISTRIBUTION OF TARDIGRADA IN SEVEN TYPICAL SERIES OF 10 CC. SAND SAMPLES

Distances from water's edge (stations) indicated horizontally in cm. Eight successive samples, each one cm. in thickness, taken between surface of sand and a depth of eight cm. at each station. Results expressed as number of Tardigrada per 10 cc. sand sample.

Beach and date	Depth of sample, cm.	Distance from water's edge, cm.								
		0	30	60	90	120	150	180	210	240
Mendota May 18, 1936	1	..	..	..	1	...	...	...	1	...
	2	..	..	1	1	...	1	2	...	...
	3	..	..	..	..	...	3	...	2	...
	4	..	..	..	..	1	1	...	...	...
	5	..	..	..	..	1	2	...	...	...
	6	..	..	..	..	2	1	...	...	...
	7	..	..	..	..	...	...	1	...	...
	8	..	..	..	..	...	...	...	...	...
		0	50	100	150	200	250	300	350	
N. Trout August 1, 1937	1	..	...	...	...	...	...	...	...	
	2	..	...	...	...	...	...	2	...	
	3	..	...	...	...	...	...	1	...	
	4	1	...	...	...	...	...	...	1	
	5	..	...	...	...	...	...	...	...	
	6	..	...	...	...	...	...	...	...	
	7	..	...	...	...	...	...	...	...	
	8	..	...	...	...	...	...	...	...	
		0	50	100	150	200	250	300		
N. Trout July 4, 1937	1	..	...	...	1	...	...	1		
	2	..	...	1	...	...	1	3		
	3	..	...	...	...	1	2	8		
	4	..	1	...	...	...	...	11		
	5	..	...	...	...	4	...	5		
	6	..	...	...	...	...	...	10		
	7	..	...	...	...	...	...	10		
	8	..	...	...	...	...	...	8		
		0	50	100	150	200	250	300		
Pallette July 11, 1937	1	..	...	...	...	...	...	...		
	2	..	...	2	5	...	1	1		
	3	..	...	...	27	3	22	1		
	4	..	...	...	6	...	...	...		
	5	..	...	...	3	...	8	3		
	6	..	...	...	...	1	...	1		
	7	3	...	...	...	...	...	...		
	8	1	...	...	...	...	...	...		
		0	30	60	90	120	150	200		
Pallette July 30, 1936	1	4	10	44	20	1	3	2		
	2	5	5	66	73	3	4	...		
	3	4	6	26	29	10	1	1		
	4	8	2	17	20	18	4	3		
	5	8	...	8	7	12	32	4		
	6	..	1	...	11	5	48	...		
	7	..	...	...	9	...	4	2		
	8	..	...	...	4	...	...	...		
		0	50	100	150	200	250			
Day July 27, 1937	1	..	409	315	147	1	...			
	2	6	232	42	100	8	...			
	3	3	13	11	3	...	2			
	4	..	4	6	...	4	...			
	5	..	...	1	...	...	...			
	6	..	1	...	...	...	...			
	7	..	...	...	...	...	...			
	8	..	...	...	...	...	...			
		0	25	50	75	100				
Plum July 22, 1936	1	..	27	34	1	1				
	2	1	17	2	1	...				
	3	2	40	1	1	...				
	4	1	75	...	...	...				
	5	..	31	...	...	...				
	6	..	22	...	...	...				
	7	..	10	...	...	...				
	8	..	2	...	...	...				

mens in the 300 cm. samples and only 11 scattered in the samples nearer to the water. The only other series to show this phenomenon was collected at Mendota on Sept. 1, 1936 when 119 specimens were found at the 200 cm. station and 35 in the rest of the samples.

In the last group may be placed the collections having a number of individual 10 cc. sand samples which contained more than 40 specimens. This condition is shown in Table 15 for Pallette on July 30, 1936 and Day on July 27, 1937. In the former series there was an average of nearly 10 tardigrades per sample. They were especially numerous at the 60, 90, and 120 cm. stations where 161, 173, and 96 specimens were found, respectively. The largest population of all was found at Day. At that beach most of the tardigrades were found in the top 2 cm. of the 50, 100, and 150 cm. stations. In these six samples a total of 1245 specimens was found with a maximum of 409 in the top cm. at the 50 cm. station. The second highest was 315 specimens in the top cm. at the 100 cm. station. Only nine specimens were found at the 0 cm. station and 13 at the 200 cm. station. Large populations were also found at Pallette in 1938 and in one series at each of the following beaches: Boulder and E. Crystal in 1936, SW. Trout, NE. Muskellunge, and Starrett in 1937.

VARIABILITY OF TARDIGRADE POPULATIONS

From the data already presented it will be noted that the populations of Tardigrada in any beach are almost unpredictable and that they may vary greatly over a period of time. This is perhaps most striking at Day beach. In 1936 between the water's edge and the 100 cm. station only seven specimens were found but almost exactly one year later very large numbers were present, over 1000 being found in the same width of the beach. Comparable variations were found at E. Crystal and Pallette. At the former, a relatively large population (367 specimens) was found between the water's edge and the 200 cm. station on July 9, 1936, but in the following year only 80 were found in the same area. In two series taken at this beach in 1938, 103 specimens were found on July 3 and only a single one on August 23. At Pallette a large population was found on July 30, 1936 but only 51 specimens in the following year. Less pronounced variations were found in some series at SW. Trout, Boulder, NE. Muskellunge, and Weber beaches.

The greater variations occurred only in the beaches of the soft-water lakes and the data gathered during the course of this investigation cannot explain this phenomenon, either on the basis of physical or chemical observations. We may easily infer that the populations of Tardigrada are not distributed in the same manner in adjacent portions of the same beach at the same time, although we have little data to support this belief.

Series of samples collected at Monona, Mendota, Plum, Trout, Superior, and White Sand beaches were quite similar in that they usually contained small numbers of Tardigrada and that there was comparatively little variation in the populations from time to time. The presence of very few organ-

isms at Monona may be explained by the youth of the beach. Since its formation in 1936 there had probably not been sufficient time for a population of tardigrades to become established. The complete absence of these organisms at Michigan and Superior is without doubt due to the very low supply of food materials in these beaches, there being only 0.6 and 0.4 mg. of organic matter per 10 cc. sand sample, respectively. The minimum amount of food material necessary for these organisms must be very low indeed since large populations were found at E. Crystal and NE. Muskellunge in spite of the fact that those beaches had mean organic contents of only 1.0 and 1.1 mg. per 10 cc. sand sample. Much of these small amounts was composed of edible algae rather than the finely divided debris found at Michigan and Superior. Although the beaches of soft-water lakes contain large quantities of desmids and filamentous algae, they are also abundant in the beaches of hard-water lakes so as to provide a sufficient food supply.

In spite of the fact that there appears to be no definite explanation for the larger populations of Tardigrada in the beaches of soft-water lakes, there are several important facts which may cast some light on the matter:

1. With the exception of Plum beach, on a hard-water lake, the large numbers of Tardigrada were all found in beaches having the finer grades of sand. Monona, already accounted for, was the only beach having fine sand that did not have a sizeable population.

2. Except for NE. Muskellunge, the larger numbers were usually found on beaches where there was little exposure to wave action.

3. The chemistry of the interstitial water may be of some significance. The capillary water of the soft-water lake beaches is comparatively low in dissolved organic and inorganic materials in contrast to the hard-water lake beaches. This is interesting when it is recalled that tardigrades are most frequently encountered in mosses where they must rely on rainwater as a source of moisture.

SEASONAL ABUNDANCE

The nine spring, early summer, and fall series taken at Mendota during 1937 give some idea of the seasonal abundance of the tardigrades. All of these series were taken within 10 m. of each other, but the inhabited width of this beach within that distance varied from 200 to 370 cm., depending upon slope. The mean numbers of individuals per 10 cc. sand sample at Mendota and the dates of collection are as follows:

April 16	0.00
May 7	0.00
May 14	0.02
May 28	1.64
June 4	1.37
June 22	3.34
September 3	0.63
October 8	0.43
November 12	0.00

Although only one specimen was found on May 14, 87 occurred in the samples taken just two weeks later. Apparently temperature conditions were sufficiently favorable during those two weeks to permit eggs to hatch out and wintering-over individuals to resume activity. A maximum population of 3.34 per sample was found late in June. By November 12 no active tardigrades were found, since freezing weather had been frequent during the two previous weeks. A series of samples collected on May 18, 1936 at this beach had a mean population of 0.29 Tardigrada per sample. This corresponds well with the series of 1937. On September 1, 1936, however, the fall decrease had not yet made its appearance, and an average population of 3.21 tardigrades per sample was found.

HORIZONTAL DISTRIBUTION

In contrast to the copepods and rotifers, the horizontal distribution of the tardigrades was quite sporadic. The variety of conditions found has already been indicated and the results shown in Tables 14 and 15. Four general types of distribution were found: concentrations near the water's edge, concentrations at the outer portions of the beach, concentrations at various points between these two extremes, and more homogeneous populations over a wide portion of the beach. Apparently the amount of capillary water in the sand as well as the slope of the beaches are by no means limiting factors in tardigrade distribution, since large numbers were found anywhere between the saturated sand at the water's edge and the outer portions of the beaches where the sand was only 20% saturated.

On the basis of 23 sets of eight vertical samples each taken from the submerged sand 20 to 50 cm. below the water's edge at a number of beaches, we may conclude that this is not a favorable environment for Tardigrada. In 16 of these sets of samples no specimens were found, but at Starrett in 1938, 22 were found and at Pallette in the same year 11 were found. Smaller numbers were found in the other five sets of samples. The submerged sand contained only 27% as many tardigrades as the samples at the 0 cm. stations and all specimens were found in the top cm.

Because of the great variations found from time to time and from beach to beach, calculations of the mean horizontal distribution of the tardigrades are of little significance. Nevertheless, the following figures will serve to give a rough picture of the situation: If 10 cc. sand samples to a depth of 8 cm. be taken at 50 cm. intervals on an "average" beach having an inhabited width of 350 cm., about 8% of the total number of tardigrades in the 64 samples will be found at the 0 cm. station, 69% will be found in the sand between 50 and 150 cm. from the water's edge, 22% will occur between the 200 and 300 cm. stations, and 1% will be found at the 350 cm. station.

VERTICAL DISTRIBUTION

In spite of numerous irregularities, it may be said that the vertical distribution of Tardigrada in the sand was more uniform than the horizontal

distribution. In some instances, however, such as at Day in 1937, the great majority (96%) was found in the uppermost 2 cm. of sand. In others, sizeable portions of the populations were found 4, 6, or 8 cm. deep, regardless of the distance from the water's edge. At N. Trout on July 4, 1937, for example, 55% were found below a depth of 4 cm. and at NE. Muskellunge on July 13, 1937, 50% were in the same region. For the most part, very few of these organisms were found as deep as 8 cm. Table 16 shows the mean vertical distribution for all series of samples taken during 1936 and 1937. These figures are comparatively low because of the incorporation of data from Michigan, Superior, E. White Sand, NE. White Sand, E. Muskellunge, and spring and fall samples from the Madison beaches where few or none were found. From this table it will be seen that 35% of all tardigrades were found in the top cm. of sand, 78% in the top 3 cm., and only 1% in the 8th cm. from the surface. Many samples were taken below 8 cm. but in most cases no Tardigrada were found, although a few samples contained two or three specimens.

TABLE 16. MEAN VERTICAL DISTRIBUTION OF TARDIGRADA, COLLECTIONS OF 1936 AND 1937. (After Pennak, 1939b.)

Depth in sand, cm.	Tardigrada per 10 cc. sand sample	Percent
1	6.5	35
2	5.5	29
3	2.7	14
4	1.6	9
5	1.1	6
6	0.7	4
7	0.4	2
8	0.2	1

The presence of these organisms in the deep layers of the sand, especially in the middle beaches, where dissolved oxygen is very low and sometimes absent emphasizes their ability to lead a facultative anaerobic existence. Moreover, it is paradoxical to find them below a depth of 3 cm. where living algal cells, an important food source, are nearly absent.

This investigation has demonstrated that wave action has little effect so far as washing the tardigrades into the deeper layers of the sand is concerned. On the days after strong onshore winds the vertical distribution picture was usually not significantly changed, although there were some indications that numbers were washed out of the upper 2 cm. of sand and back into the lake.

COPEPODA

Although copepods have long been known to inhabit such unusual environments as marine algae, fresh-water mosses, other aquatic plants, and even the mosses of forests, far removed from any body of water, it has been

only recently pointed out by Wilson (1932) that the sandy beaches of lakes, ponds, and ocean support a great variety of copepods. In these areas in the vicinity of Woods Hole, Massachusetts, he found many undescribed species, as well as others which had been previously reported from the sandy ocean bottom. Because of their peculiarities and unique environment, Wilson has applied the term "terraqueous" to the group of Copepoda which inhabit muds and sands, whether on the beach or submerged. Further work on the copepods inhabiting ocean beaches has been carried out at the marine station at Millport, Scotland, by Nicholls (1935). He reported eight new species, along with others. According to both of these authors, the different species have an almost specific distribution, from low water to the highest part of the beach which is submerged by the tides only for short periods. Nicholls found that some of the species were restricted vertically, some of them being found only in the top 3 cm. of sand, while others were found in the deeper layers.

Wilson (1935) has admirably discussed the terraqueous Copepoda in relation to those found in other environments, so there is no need for a lengthy discussion here. Briefly, the copepods found in the sand, with the exception of one species, all belong to the Harpacticoida. These sand-dwelling forms are very feeble swimmers, and depend on worm-like wriggling movements for locomotion. They move about incessantly in the capillary water between the sand grains without displacing them. Because of this continual motion it is impossible to identify the living animals. Their transparency renders them almost invisible in the sand when observed under the binocular microscope.

Morphologically, the sand-dwelling copepods are modified in several ways which fit them to their surroundings. First, they are all quite small; slightly more than 700 μ is the maximum length attained by any of the species. Second, these copepods are greatly modified as to general body shape, being elongated and worm-like. Third, they are very flexible, there being considerable freedom of movement in all of the articulations. Fourth, there are well-developed tactile structures, particularly in the form of aesthetasks, which are often enlarged and numerous on the antennae; these may be supplemented by strong hastate setae. Fifth, the plumose setae, so characteristic of the legs of the free-swimming copepods, are replaced by strong, stiff spines.

In contrast to the large number of species found in the beaches of ocean and brackish waters, the work on the beaches of the Wisconsin lakes has shown only three species. One of these, *Parastenocaris brevipes* Kessler, was nearly universal in occurrence, being absent only from Michigan. *Parastenocaris starretti* Pennak occurred at Starrett and NE. White Sand. *Phyllognathopus paludosus* Mrazek was found only at Starrett in 1937. *P. brevipes* was first discovered in damp moss on the slopes of moraines in Germany; it has been found several times since, usually in sphagnum. Wilson found it "in the sand an inch or more beneath the surface and close to the

water's edge" in the beaches of two small, fresh water ponds near Woods Hole. A description of *P. starretti* and an account of its distribution in the beach at Starrett lake has been presented by Pennak (1939a). *P. paludosus* has been reported several times from lakes, springs, and mosses. Mrazek found it in damp moss and marshy places near Prague. Chappuis found it in moss samples in Jugoslavia. Wilson described it as being found in fresh water and subterranean in habitat.

In this study the copepods in the samples were counted and tabulated, every individual which was more advanced than the naupliar stages being regarded as an adult. Younger individuals were not counted in with the regular adult population. The mean proportion of immature forms was less than 5%.

GENERAL DISTRIBUTION

In most beaches the distribution of the copepods was quite characteristic with the greatest numbers being found between 90 and 300 cm. from the water's edge where the sand was neither saturated nor too dry, and removed from the effects of most of the wave action. Table 17 shows the detailed distribution of Copepoda in seven typical series of samples from five different beaches, all of which contained comparatively large numbers, and Table 18 is a summary of the copepod distribution in the 66 series of collections. The most striking fact brought out by these data is the great variation in numbers, from hundreds of specimens in such beaches as N. Trout and Pallette to very few or none at Monona, Arbor Vitae, Weber, and Michigan. So far as individual sand samples are concerned, N. Trout, Pallette, Mendota, S. Trout, Starrett, and E. Crystal all had samples which contained more than 50 specimens. The greatest number found in any one sample was 277 at N. Trout on August 1, 1937 at a depth of 2 cm. at the 200 cm. station.

Two series taken at SW. Trout up to 125 cm. from the water's edge in 1936 contained only eight specimens, but in 1937 in a wider portion of this beach 33 specimens were found at the 160 and 200 cm. stations. At Day beach in 1936 none were found as far back as 100 cm., but in 1937 when a series of samples was taken in a wider portion of this beach just 5 m. away, 60 individuals were contained in the 16 samples collected at the 200 and 250 cm. stations. Comparable variations due to beach width were found at SW. Trout and E. White Sand. Arbor Vitae, Plum, Boulder, and W. Crystal are all narrow beaches, and, as will be emphasized later, there is no opportunity for sizeable populations to become established. In these narrow beaches, samples were often taken from the sandy soil beyond the limit of the true beach, but very few copepods were found there.

Only four specimens were found in the two summer series collected at Monona although samples were taken as far back as 250 cm. from the water's edge. Such small numbers may be due to the fact that the beach had been in existence only one year, so that there had not been sufficient time for these

TABLE 17. DISTRIBUTION OF COPEPODA IN SEVEN TYPICAL SERIES OF 10 CC. SAND SAMPLES

Distances from water's edge (stations) indicated horizontally in cm. Eight successive samples, each one cm. in thickness, taken between the surface of the sand and a depth of eight cm. at each station. Results expressed as numbers of Copepoda per 10 cc. sand sample. Asterisk indicates point on surface of sand which was about 12 cm. above surface of the lake.

Beach and date	Depth of sample, cm.	Distance from water's edge, cm.							
		0	50	100	150	200	250	300*	
E. Crystal July 8, 1937	1	..	..	12	...	...	3	...	
	2	..	2	...	2	14	...	...	
	3	..	..	...	2	30	...	...	
	4	..	..	...	...	19	...	...	
	5	..	..	...	...	14	...	...	
	6	..	..	...	...	8	5	...	
	7	..	..	...	...	...	2	...	
	8	..	..	...	...	2	...	...	
		0	50	100	150	200	250	300*	
Pallette July 11, 1937	1	..	..	...	...	3	...	...	
	2	..	..	...	43	4	10	...	
	3	..	..	...	157	31	31	3	
	4	..	..	...	11	48	7	4	
	5	..	..	...	2	8	7	2	
	6	..	..	...	1	5	26	...	
	7	..	..	...	...	15	9	1	
	8	..	..	...	...	2	8	...	
		0	50	100	150	200*	250	300	350
E. White Sand July 18, 1937	1	..	..	...	...	...	2	...	...
	2	..	3	...	...	...	4	...	...
	3	..	..	...	...	...	6	...	...
	4	..	..	...	...	9	6	1	...
	5	..	..	...	1	7	8	3	...
	6	..	..	...	...	2	9	9	2
	7	..	..	...	...	5	9	9	10
	8	..	..	...	...	...	12	12	41
		0	60	120	160	200*	240	280	
S. Trout Aug. 13, 1936	1	..	4	...	...	36	26	6	
	2	..	1	...	9	35	8	2	
	3	..	4	...	1	22	3	1	
	4	..	..	...	1	18	10	...	
	5	..	..	...	...	9	4	...	
	6	..	..	...	...	2	...	...	
	7	..	..	...	...	...	...	...	
	8	..	..	...	...	...	...	...	
		0	50	100	150	200*	250	300	
N. Trout Aug. 17, 1937	1	..	1	...	3	5	21	...	
	2	..	6	7	5	54	14	5	
	3	1	2	3	2	137	9	10	
	4	6	..	...	...	125	2	11	
	5	7	..	...	...	42	1	11	
	6	6	..	...	...	29	5	14	
	7	6	..	...	...	2	10	2	
	8	3	..	...	...	...	3	...	
		0	50	100	150*	200	250	300	
N. Trout Aug. 1, 1937	1	..	1	9	108	120	49	2	
	2	2	..	23	113	277	119	2	
	3	1	..	2	74	196	25	35	
	4	..	2	...	30	189	15	37	
	5	1	5	...	35	9	2	24	
	6	..	5	...	12	78	...	23	
	7	..	12	...	32	4	1	10	
	8	..	4	...	5	4	...	...	
		0	30	60	90*	120	150	180	210
E. Crystal July 9, 1936	1	..	..	6	124	6	15	1	...
	2	..	4	17	28	42	6	3	...
	3	..	..	3	10	75	12	1	...
	4	..	4	...	10	71	4	2	...
	5	..	3	1	8	14	2	...	...
	6	..	..	...	2	2	6	1	...
	7	..	..	...	...	1	2	...	...
	8	..	..	...	...	...	...	...	...

organisms to become established. Since data are not available for some of the natural beaches at this lake, no definite conclusions can be drawn, but from comparisons with beaches similar in all other aspects a larger copepod population would be expected.

The absence of copepods at Michigan may be due to the fact that the samples were taken before the spring appearance of the copepods, or it may be due to the low food supply in the sand.

In spite of the fact that the copepod populations were comparatively stable in comparison with the tardigrades, there were a few instances where large variations were found at different times within the same beach. At Superior on August 8, 1937, none were found, but in the following year on July 17, 65 specimens were present. E. Crystal showed the greatest variation. On July 3, 1938, 528 copepods were found in 48 samples taken between the water's edge and the 250 cm. station. Just about seven weeks later only three were found at the same stations. As in the case of the Tardigrada, the causes of these variations are yet to be determined.

Although N. Trout and S. Trout are almost identical, differing markedly only in the relative amounts of wave action, about three times as many copepods were found in the former as in the latter. This estimate is based on ten and six series, respectively. The amount of wave action, however, may not be a direct governing factor. Food, oxygen, amounts of capillary water, or some other influence are likely to be of more direct importance.

Mean numbers of copepods found in the various beaches give a rough conception of the range encountered. N. Trout had by far the greatest population with an average of 14.45 copepods per 10 cc. sand sample. Pallette had the second highest with 7.26 per sample. Starrett and E. Crystal also had large numbers, from five to seven per sample. NE. White Sand, S. Trout, E. Muskellunge, E. White Sand, Mendota, and NE. Muskellunge had medium populations, from one to five per sample. All other beaches had less than one individual per sample, and none were found at Michigan. It must be recalled, however, that W. Crystal, Boulder, Arbor Vitae, and Plum are too narrow to harbor any numbers of these organisms. The generally low mean populations are due, of course, to the fact that samples from the inner and outer portions of the beaches as well as the deep sand samples were taken into consideration in calculating the mean populations.

As measured by the total particulate organic matter, the likelihood of available food in the sand being a limiting factor is doubtful. N. Trout, Pallette, Starrett, and E. Crystal all had large populations, but the particulate organic material in these beaches had almost the maximum range, from 1.0 mg. per sample at E. Crystal to 11.5 mg. at Starrett. The presence of copepods at Superior where only 0.4 mg. per sample of organic matter was found indicates that a very low food supply may suffice to support these animals.

In ponds and lakes the amount of particulate matter per liter which may

TABLE 18. SUMMARY OF DISTRIBUTION OF COPEPODA; 66 SERIES OF SAMPLES

Distance from water's edge indicated horizontally in cm. Each value represents the total number of organisms found in the eight successive 10 cc. sand samples, each one cm. in thickness, between the surface of the sand and a depth of 8 cm. Results have been interpolated in some instances where stations were not established at 50 cm. intervals.

Beach	Date	Distance from water's edge, cm.								
		—50	0	50	100	150	200	250	300	350
Monona	June 28, 1937	0	0	1	3	0	0	...	...	...
	Sept. 8, ”	...	0	0	0	0	0	...	...	...
	Oct. 29, ”	...	0	0	0	0	0	0	...	...
Mendota	May 18, 1936	...	0	1	1	0	36	1	...	...
	Sept. 1, ”	...	0	1	2	2	12	...	...	...
	Nov. 12, ”	...	0	0	0	0	0	...	...	...
	Apr. 16, 1937	...	0	0	0	0	0	0	...	...
	May 7, ”	...	1	0	0	0	0	...	...	...
	May 14, ”	...	0	0	1	0	0	0	...	...
	May 28, ”	...	0	0	8	126	68	61	...	...
	June 4, ”	...	0	0	0	0	4	8	...	...
	June 22, ”	0	0	9	2	9	3	6	...	...
	Sept. 3, ”	...	0	0	1	1	2	0	...	...
	Oct. 8, ”	...	0	0	0	0	1	14	0	...
Arbor Vitae	Aug. 5, 1936	...	2	1	0	1	...	...	...	...
Plum	July 22, 1936	...	0	0	1	...	...	...	...	...
	Aug. 19, 1938	0	0	0	0	...	...	...	...	...
N. Trout	July 5, 1936	...	0	2	89	145	...	...	...	...
	Aug. 16, ”	...	5	3	17	269	327	2	...	...
	July 4, 1937	0	1	28	34	114	193	640	5	...
	July 18, ”	...	58	49	43	415	206	129	3	...
	Aug. 1, ”	...	4	29	34	409	878	211	133	3
	Aug. 17, ”	...	29	9	10	10	394	65	53	3
	July 3, 1938	...	5	0	54	389	264	...	...	...
	July 31, ”	...	0	7	140	55	105	...	...	...
	Aug. 4, ”	0	0	3	95	119	468	...	...	...
	Aug. 26, ”	0	22	9	4	25	293	112	...	...
S. Trout	July 19, 1936	...	0	0	0	30	129	...	...	...
	Aug. 13, ”	...	0	2	3	9	122	41	2	...
	July 5, 1937	...	0	0	10	72	29	18	1	...
	Aug. 15, ”	...	1	3	0	1	4	72	116	...
	July 12, 1938	0	0	0	0	68	264	...	...	...
	Aug. 15, ”	0	0	3	5	26	70	...	...	...
SW. Trout	July 19, 1936	...	0	0	4	...	...	...	...	...
	Aug. 13, ”	...	0	4	0	...	...	...	...	...
	July 23, 1937	...	0	0	0	1	32	...	...	...
Michigan	May 29, 1937	...	0	0	0	0	0	0	0	...
Superior	Aug. 8, 1937	...	0	...	0	...	0	0	0	0
	July 17, 1938	0	0	0	2	6	2	55	...	...
E. White Sand	July 22, 1936	...	0	0	2	...	...	...	...	...
	July 18, 1937	...	0	3	0	1	23	56	34	53
	July 24, 1938	...	0	0	0	0	5	35	50	...
NE. White Sand	Aug. 18, 1938	...	0	0	31	23	24	151	...	...
Boulder	Aug. 2, 1936	...	1	5	7	...	...	...	...	...
	Aug. 14, 1937	...	0	1	...	...	...	...	...	...
	July 24, 1938	0	0	0	0	0	...	...	...	...
NE. Muskellunge	July 16, 1936	0	0	0	3	0	...	...	...	...
	Aug. 21, 1936	...	0	0	0	1	19	61	...	...
	July 13, 1937	...	0	1	3	0	...	...	...	...
	Aug. 22, ”	...	0	0	3	2	45	10	4	...
E. Muskellunge	July 31, 1938	0	5	8	126	0	0	...	...	...
	Aug. 13, ”	0	0	0	159	0	0	0	...	...
Pallette	July 30, 1936	...	8	2	15	93	6	...	...	...
	July 11, 1937	...	0	0	0	214	116	98	10	...
	July 10, 1938	0	0	4	12	60	440	...	...	...
Weber	July 29, 1936	...	0	0	0	...	...	...	...	...
	Aug. 11, ”	...	0	0	0	2	0	...	...	...
Starrett	July 30, 1937	...	0	0	18	74	352	...	...	...
	Aug. 7, 1938	0	0	29	110	2	0	...	...	...
Day	Aug. 2, 1936	...	0	0	0	...	...	...	...	...
	July 27, 1937	...	0	0	0	0	49	11	...	...
W. Crystal	July 9, 1936	...	0	5	...	...	...	...	...	...
E. Crystal	July 9, 1936	...	0	22	188	47	6	...	...	...
	July 8, 1937	...	0	2	12	4	87	10	0	...
	July 3, 1938	0	33	28	41	65	358	3	...	...
	Aug. 23, ”	0	0	2	1	0	0	0	...	...

serve as a food source is only a small fraction of what it is in the capillary water. Nevertheless, the planktonic copepods are able to swim about and "strain" a much larger quantity of water than the beach copepods which are so restricted in their movements that they come in contact with a relatively small amount of capillary water.

Reference to Table 9 shows that hardness of the lake waters (as well as the capillary waters), exposure to wave action, and sand grain size have no apparent relation to the magnitude of the copepod populations.

It has already been mentioned that *Parastenocaris brevipes* was found in all beaches except Michigan. At Starrett, however, *Parastenocaris starretti* and *Phyllognathopus paludosus* were also found, both in 1937 and 1938. In the former year *P. starretti* constituted about 71% of the total population and *Ph. paludosus* accounted for about 7%. In the latter year, these figures were 90% and 2%. *Ph. paludosus* was found only at the 100 cm. station, but the other two species were present from the 100 to 200 cm. stations. *P. starretti* was the dominant form at NE. White Sand also; 92% of the copepods were this species.

Twenty-three of the samples collected at a number of beaches contained sufficiently large numbers of copepods to permit a reliable estimate of the relative numbers of males and females. The percentage of males in these samples ranged from 2.7% to 31.0%. Both values were obtained from samples collected at S. Trout on August 15, 1937. The mean for all counts was 17.7% males. No relationships between male production and any physical, chemical, or biological factors were noted.

In the beach at Lake Mendota the copepod populations showed evidence of a spring maximum. Largest numbers were found during the last two weeks of May. Samples taken earlier contained very few specimens and later samples in both spring and fall contained small numbers. July and August samples collected at the other beaches demonstrated no population cycles although some of the late August series contained noticeably smaller numbers than those collected earlier in the summer.

HORIZONTAL DISTRIBUTION

Knowing the width and degree of slope of a beach, it is possible to predict to some extent the area in which the majority of the copepods will be found. Apparently these organisms respond to an optimum amount of water in the sand, being almost entirely absent within 50 cm. of the water's edge where the sand is almost completely saturated, and from the outer regions where the sand is too dry. This concentration of copepods in the middle beaches is shown in Tables 17, 18, and 19.

Furthermore, the distribution is apparently governed by the slope of the sand. In beaches having abrupt slopes (7°, for example) and consequently narrow inhabitable portions of the sand, the major portion of the copepods were found to be concentrated between the 50 and 150 cm. stations. Certain

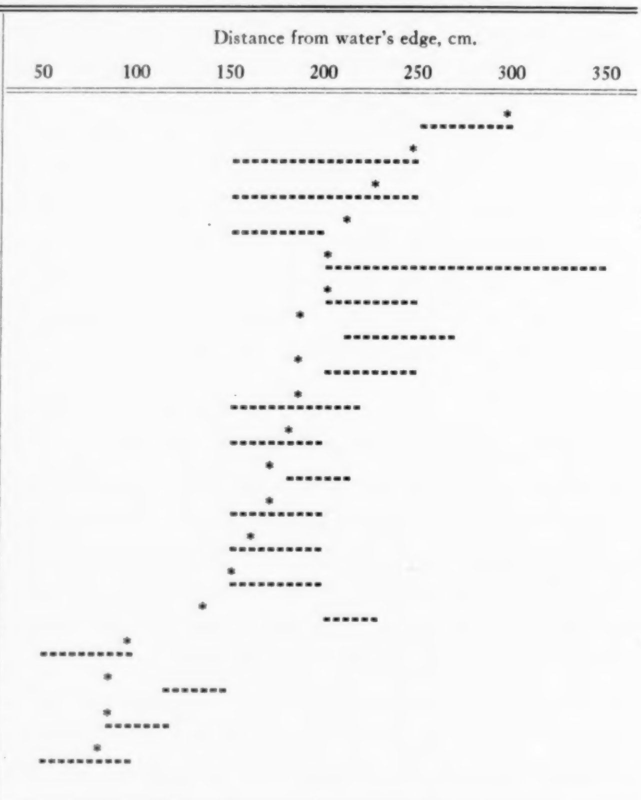
collections at Starrett, Pallette, E. Crystal, and E. Muskellunge showed this condition quite plainly. Conversely, in beaches having gentle slopes (3°) the sand was wet back farther and the copepods were found at greater distances from the water's edge. In certain collections at E. White Sand, S. Trout, N. Trout, and Pallette large numbers of copepods were found as far as 250, 300, and even 350 cm. from the water's edge. This relationship between slope and distribution of Copepoda, however, is only approximate and cannot be stated as a rigid rule. At E. White Sand, for example, on July 18, 1937 (Table 19), large numbers were found between 200 and 350 cm. from the water's edge despite the fact that the slope was not particularly gradual. This was due to a comparatively flat area beyond 200 cm., which served to increase the horizontal extent of the damp sand.

Table 19 emphasizes the importance of measuring slope when samples are collected. Two transects of a beach only 5 or 10 m. apart may differ markedly in the slope and consequently in the amounts of water in the sand. This variation is shown by the three series for Pallette which were all taken within 15 m. of each other.

TABLE 19. RELATIONSHIP BETWEEN BEACH SLOPE AND COPEPOD POPULATIONS IN 19 DIFFERENT SERIES OF SAMPLES

Extent of horizontal lines indicate regions in which majority of copepods were found. Asterisks indicate points on surface of sand which were 12 cm. above the surface of the lake.

Beach	Date
S. Trout	Aug. 15, 1937
Pallette	July 11, 1937
N. Trout	July 4, 1937
N. Trout	Aug. 4, 1938
E. White Sand	July 18, 1937
N. Trout	Aug. 26, 1938
NE. Muskellunge	Aug. 21, 1936
N. Trout	Aug. 17, 1937
Mendota	June 28, 1937
N. Trout	July 3, 1938
Mendota	May 18, 1936
Pallette	July 10, 1938
E. Crystal	July 3, 1938
N. Trout	Aug. 1, 1937
S. Trout	July 12, 1938
Starrett	Aug. 7, 1938
Pallette	July 31, 1936
E. Crystal	July 9, 1936
E. Muskellunge	July 31, 1938



The summer of 1936 was comparatively dry and some of the lake levels fell sufficiently between July 10 and August 20 to expose an additional 50 or 100 cm. of sand. This resulted in the movement of the inhabitable portion of the beaches in a lakeward direction. At both N. Trout and S. Trout it was found that the populations of copepods migrated lakewards as the water level fell.

In the majority of instances very few copepods were found at the 0 and 50 cm. stations. At N. Trout, however, comparatively large numbers were sometimes encountered in those regions. This condition was found to be due to heavy wave action. Receding waves served to carry lakewards numbers of eggs and nauplii, as well as some adult forms.

Although numerous sand samples were collected from the submerged sand 50 cm. from the water's edge, no copepods except a few planktonic Cyclops were found.

VERTICAL DISTRIBUTION

The vertical distribution of the copepods was quite characteristic, with most of them being found in the uppermost 4 cm. of the sand. Table 17 shows this typical distribution in seven different series of samples. Certain flat beaches did not show this distribution very clearly. At the more distant stations of these beaches the upper portions of the sand were too dry and many of the organisms were found in maximum numbers below a depth of 4 cm. Such a situation is shown (Table 17) at E. White Sand on July 18, 1937, when the deep samples at the 300 and 350 cm. stations contained the majority of the copepods.

Figure 10 is a summary of the vertical distribution of Copepoda collected at 16 beaches during 1936 and 1937. Seven of these (Plum to W. Crystal) contained small numbers with an average of less than one per sample, but nevertheless the great majority were found in the uppermost 4 cm. of sand (except at SW. Trout). Day showed a maximum of 3.8 copepods per sample at a depth of 3 cm., but only 0.9 were found in the surface samples and none in the bottom 2 cm. At Mendota and NE. Muskellunge the vertical distribution was more homogeneous than at any of the other beaches. At the former, a maximum of three per sample was found at a depth of 5 cm., and the surface and bottom samples contained 0.9 and 0.2 per sample, respectively. In the latter beach, 0.3 were found in the surface sample and 0.7 in the bottom sample, with a poorly defined maximum of 1.5 at a depth of 3 cm. Starrett, E. Crystal, N. Trout, and S. Trout were more typical with large numbers of copepods at or near the surface of the sand and few in the deeper samples. The large population at Pallette had an unusual distribution. Only 0.7 and 1.3 copepods per sample were found in the surface and bottom samples, respectively, but a well-defined maximum of 19.3 was found at a depth of 3 cm. An extreme condition, already mentioned, was found at E. White Sand; the top three samples each averaged less than one

specimen, but the samples 7 and 8 cm. deep contained 4.1 and 8.1 specimens, respectively.

Of nine beaches having the larger numbers of copepods, the proportion of the total population found in the top 4 cm. of sand ranged from 20% at E. White Sand and 44% at Mendota to 86% at E. Crystal and 90% at Day.

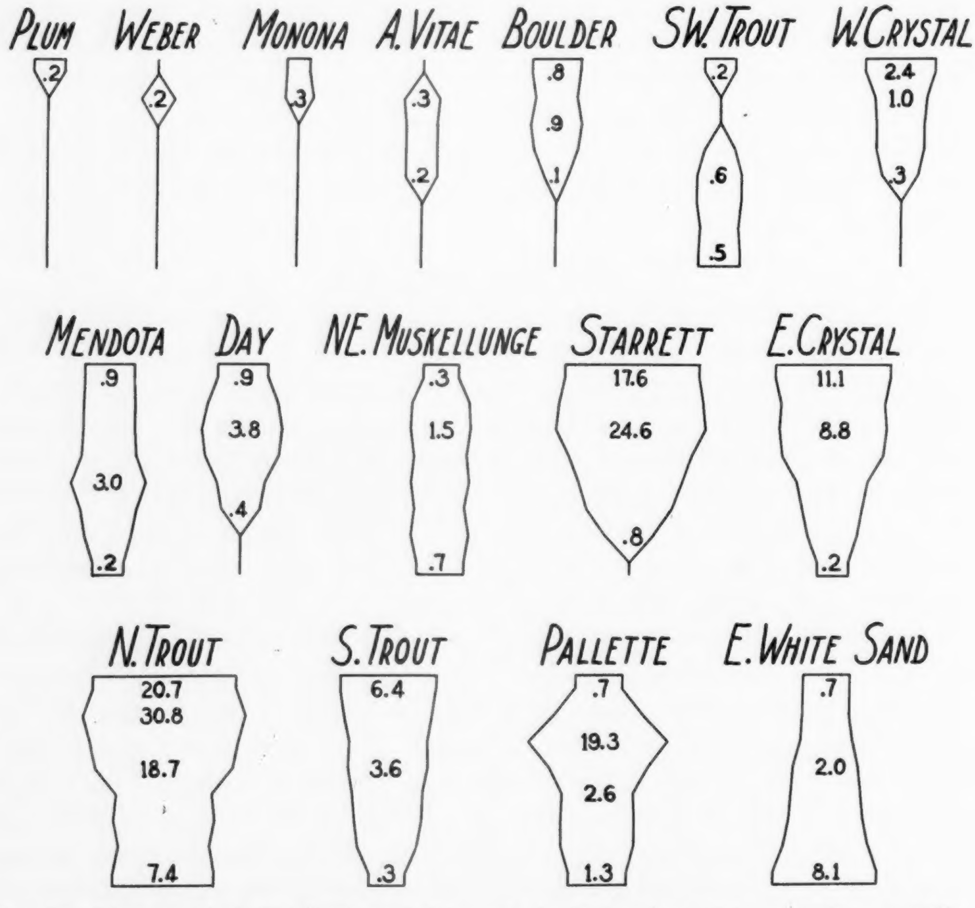


FIG. 10. Mean vertical distribution of Copepoda in 16 beaches; data of 1936 and 1937. Results expressed as number of copepods per 10 cc. sand sample.

Series of samples taken after periods of both calm and heavy wave action show that waves wash only a small portion of the organisms out of the surface layers of the sand. Although the data are very incomplete, there is evidence to show that even a hard all-day blow will remove less than 30% of the Copepoda out of the top 3 cm. of sand back into the lake. A blow of two or three days duration, of course, may remove a larger portion. After a period of several comparatively calm days, however, the normal vertical distribution is restored. Apparently the copepods respond to optimum conditions near the surface. There are no data to show that waves and rains

wash the copepods into deeper portions of the sand. This may be prevented in a large measure by the small size of the spaces between the sand grains.

Some copepods were found below a depth of 8 cm., especially at N. Trout, E. White Sand, and Pallette, but these numbers were usually small compared with the samples taken from the surface. In several instances a few stragglers were found at a depth of 11 cm.

From the standpoint of this study, pH, dissolved oxygen, dissolved carbon dioxide, dissolved organic and inorganic materials, and grade of sand have no apparent influences on numbers and distribution of the Copepoda. Indeed, in a few cases these organisms were taken from sand containing quantities of ferrous sulphide.

ROTATORIA

Although there are many workers interested in the biology of the Rotatoria, the probability of sandy beaches harboring these organisms has gone unnoticed until recently. Chiefly as the result of Wiszniewski's work in Poland and Myers' work on the rotifers of the sandy beaches of two small, highly colored lakes in the pine-barren area in southern New Jersey, 205 different species are known from the sand. Of these, 105 were reported from Poland and 145 from New Jersey.

This paper, however, is not drawn up along taxonomic lines but is an attempt to present some conception of the numbers and distribution of the various species in the sand together with observations on the influences exerted by the peculiar environmental conditions. Species identifications were made in most cases while counting the organisms. Uncertain specimens were mounted permanently in glycerin for a closer study. Where necessary, a mount was made of the trophi, which procedure has become a necessity for the identification of species in many genera. There is no doubt that a number of specimens were incorrectly identified due to inferior killing and fixation methods, but it is certain that the proportion of inaccuracies is under 1%. In practically all cases it is certain that the genera are correct, at any rate. A few specimens of what are undoubtedly undescribed species were found, but it is not possible to draw up adequate descriptions because they were so strongly contracted.

Wiszniewski (1934) has divided the psammolittoral Rotatoria into three general ecological groups: (1) *psammobiotic* rotifers, which are found only in the sand, elsewhere as occasional stragglers, (2) sand-loving *psammophile* rotifers, also found in the littoral regions among aquatic vegetation, and (3) *psammoxene* rotifers, alien littoral and plankton species which are found in the sand in small numbers, carried there by waves as adults or eggs which hatch but whose individuals soon die.

The Bdelloidea are not included in this section but will be briefly discussed later. The ploimate species are much more numerous and characteristic of the psammolittoral environment. Those which are strictly con-

fined to beaches (psammobiotic species) are not modified in any manner which differentiates them from the majority of rotifers. In a few species, however, there is considerable dorsoventral or lateral constriction such as in *Euchlanis arenosa* and *Cephalodella compacta.* In others, such as *Encentrum insolitum,* there are strongly developed foot glands which enable them to adhere firmly to the sand particles. Some species, like *Lecane inquieta,* are characterized by their great rapidity of movement.

ROTATORIA FOUND IN THE WISCONSIN LAKE BEACHES

Psammoxene species

In the present study, as well as in those of Myers and Wiszniewski, the psammoxene rotifers constituted the majority of the total number of species encountered. They were usually found in very small numbers in the region of the hygropsammon, and, because their occurrence there is accidental, they are not treated in this investigation. Some of the more common psammoxene genera and species are: *Keratella cochlearis* (Gosse), *Polyarthra trigla* (Ehrenberg), *Euchlanis dilatata* (Ehrenberg), Ploesoma, Synchaeta, Testudinella, Notholca, and Brachionus. Theoretically, it is possible that all of the plankton and littoral species characteristic of a body of water may be found in its beaches, carried there by waves and currents, either independently or on aquatic plants washed upon the shore. So far as is known, they do not reproduce in the sand to any extent. It was noticed that after several days of offshore winds at the Wisconsin lakes the psammoxene species disappeared almost entirely from the sand. On the other hand, there were no accompanying significant changes in the numbers of psammobiotic and psammophile forms.

Psammophile species

The distinction between psammoxene and psammophile species is by no means clear, but the two groups may be roughly separated on the basis of their numbers and distribution in the sand. Large numbers of the latter group are found living and reproducing as far back as 250 to 350 cm. from the water's edge. The few living psammoxene rotifers encountered were almost always found within 100 cm. of the water's edge. Table 20 is a summary of the relative numbers and distribution of the psammophile rotifers encountered in the Wisconsin study. Following is a list of these species with pertinent remarks concerning their distribution.

Aspelta circinator (Gosse) has not been previously reported from sandy beaches. A few specimens were found in five of the beaches and at E. Crystal on July 8, 1937 a large crop was present, with one sample at the 250 cm. station containing more than 60.

Bryceella tenella (Bryce) was common in the beaches of the Polish and New Jersey lakes but only two examples were found at SW. Trout in the Wisconsin investigation.

Cephalodella apoceola Myers was seldom found. It occurred only at Starrett and W. Crystal.

Cephalodella auriculata (Müller) was found scattered in the hygropsammon in small numbers at most beaches and in medium numbers at Monona and Mendota during the spring months. Wiszniewski also found maximum populations in the spring.

Cephalodella catellina (Müller) was abundant in both spring and fall collections at Monona when more than 50 specimens were found in some samples. Medium numbers occurred at Mendota and a few were found in five other beaches. Like *C. auriculata*, this species is confined to the hygropsammon.

Cephalodella exigua (Gosse) was quite rare and was present in only five of the beaches. Myers found it to be a common inhabitant of the New Jersey beaches.

Cephalodella gibba (Ehr.) was present in small to medium numbers in nearly all beaches, being absent only at W. Crystal. In a few instances 20 to 30 per sample were found as far as 250 cm. from the water's edge.

Cephalodella gracilis (Ehr.) was scattered in medium numbers at Monona but in seven other beaches only a few specimens were found.

Cephalodella megalocephala (Glasc.) was found to be a rare inhabitant in the hygropsammon of ten beaches.

Cephalodella remanei Wisz. was found rarely at Mendota, N. Trout, S. Trout, and Pallette. It was absent from all of the other beaches.

Colurella colurus (Ehr.) occurred in small to medium numbers in all beaches in both the hygropsammon and eupsammon.

Colurella obtusa (Gosse) was found rarely in most of the beaches.

Colurella uncinata (Müller) was found rarely in most of the beaches.

Dicranophorus lütkeni (Bergendal), in several series of samples, numbered as many as ten individuals at Mendota, Starrett, N. Trout, and W. Crystal. It occurred rarely in three other beaches and was absent from the remainder.

Dicranophorus prionacis (Stenroos) was scattered evenly in the hygropsammon and eupsammon of most beaches in small to medium numbers. This species is listed by neither Myers nor Wiszniewski, but because of its wide distribution, the present writer regards it as a distinct psammophile.

Elosa worralli Lord was found rarely at Pallette and Day beaches. Myers reported it as being common in New Jersey.

Lecane clara (Bryce) was found in only five beaches. Usually two or three specimens were found in each series of samples. Myers reported it as being common in New Jersey and Wiszniewski reported it as being very abundant in the Polish beaches.

Lecane[2] *closterocerca* (Schmarda) was found in small to medium num-

[2] Following the suggestions of Edmondson (1935) the genera Lecane and Monostyla have been joined into one genus, Lecane. Trichocerca and Diurella are likewise grouped together as Trichocerca.

bers in most of the beaches and in a few instances as high as 40 per 10 cc. sand sample. Horizontally, it was found as far as 200 cm. from the water's edge.

Lecane flexilis (Gosse) was found only occasionally in six of the beaches.

Lecane hamata (Stokes) was the most abundant species encountered in the Wisconsin beaches. In some 10 cc. sand samples more than 300 specimens were found. Wiszniewski reported finding only two specimens in the beaches of Lake Wigry and Myers classified it as a rare psammoxene. In view of the fact that large numbers were found as far as 250 cm. from the water's edge, there is no doubt that this is a psammophile species, at least in Wisconsin.

TABLE 20. RELATIVE ABUNDANCE OF PSAMMOPHILE ROTATORIA IN ALL BEACHES
1 = very abundant, 2 = numerous, 3 = medium numbers, 4 = small numbers, 5 = rare.

Beach	*Aspelta circinator*	*Bryc la tenella*	*Cephalodella apocola*	*C. auriculata*	*C. catellina*	*C. exigua*	*C. gibba*	*C. gracilis*	*C. megalocephala*	*C. remanei*	*Colurella* spp.	*Dicranophorus lutkeni*	*D. prionacis*	*Elosa worralli*	*Lecane clara*	*L. closterocerca*	*L. flexilis*	*L. hamata*	*L. inermis*	*L. luna*	*L. lunaris*	*L. nana*	*L. ohioensis*	*L. scutata*	*L. verecunda*	*Lepadella* spp.	*Monommata astia*	*Proales* spp.	*Trichocerca intermedia*	*T. tenuior*	*T. tieris*	Total number of species
Monona				3	3		3	3			4					3		4			5					4						9
Mendota				3	3	4	4	4	5	5	3	4	4		4	4	5	4		5	5		5	4		3		4	4	4	4	23
Arbor Vitae							4	5			4					4	5	1			4		4			3				4		10
Plum				5			5		4		5		4			3		2			4		4			3		3	3	4		13
N. Trout	5			5	4	4	4	4	5	5	4	4	3		5	4	5	2	5	4	4	5		3		3	5	4	3	3	4	26
S. Trout				4		5	5	5		5	4		4		4	3		1		4	5		4	2		3	4	4	2	3	5	20
SW. Trout		5		4			4		4		4	5	3			3		2	2		3	2		3	2	2		3	3	3		18
Michigan				4	4	5	3	4			4															3						7
Superior					5		4				4		4													4		5				6
E. White Sand	5			5	4		4		4		5				4	3	5	1	5	5	4		5	2		2	5	5	2	3	5	21
NE. White Sand				4	4		4		5		5						5	3		4				1		2	4	4	3	3	4	15
Boulder				5			4				5	5	3			4		3			4		5	3		4	5		4	3		14
NE. Muskellunge				4		5	4	4	5		4		4		5	4	4	3		5	3		5	3	5	3		4	4	3		20
E. Muskellunge				5			5		5		5	5						3					5	3		3	5	3	4	4		13
Pallette	5						4			5	4		5	5				2		5	4			2		3			4	3	5	14
Weber							2				4		4			3		2			3			2		3		4	3	4		11
Starrett	4		5				4		5		3	4	3			3		4	5		3			2		2			3	2		15
Day	4						4				4		4	5		4		3			3	5		2		4	5			4		13
W. Crystal			5						5		5	4									3			3		5		4	3	3	5	11
E. Crystal	3						3	4			3		4			5		4			4			2		4		4	3	3		13

Lecane inermis (Bryce) was abundant at SW. Trout, otherwise rare or absent. This is the first record of this species from a sandy beach.

Lecane luna (Müller) occurred in small numbers (up to five specimens per series of samples) in seven beaches back to a distance of 150 cm. from the water's edge. It is quite likely a true psammophile species. Wiszniewski, however, listed it as a psammoxene.

Lecane lunaris (Ehr.) occurred in small to medium numbers in nearly all beaches. Some samples contained over 30 specimens. It was listed as being rare in Polish beaches and few to common in the New Jersey beaches.

Lecane nana (Murray) was abundant at SW. Trout, rare at N. Trout and Day, and absent in all other beaches. This is the first record of this species from a sandy beach. Its distribution indicates its psammophile nature.

Lecane ohioensis (Herrick), although found in small numbers, may also be classed as a psammophile species in view of the fact that it occurred in eight beaches in both the hygropsammon and inner regions of the eupsammon.

Lecane scutata (Harring and Myers) was common to abundant in most of the beaches. Many samples contained more than 50 specimens and a few contained more than 300. Large numbers were found as far as 300 cm. from the water's edge. This species has previously been regarded as a psammoxene, but undoubtedly it is a psammophile.

Lecane verecunda Harring and Myers was numerous at SW. Trout, rare at NE. Muskellunge, and absent from the other beaches. Its occurrence as far as 150 cm. from the water's edge indicates its psammophile nature.

Lepadella ovalis (Müller) was present in small to medium numbers in all beaches.

Lepadella patella (Müller) was abundant nearly everywhere in the hydropsammon and eupsammon. Sometimes it numbered more than 200 specimens per sample.

Monommata astia Myers occurred in small numbers in seven of the beaches. Comparable conditions and distribution were reported from Poland and New Jersey.

Proales decipiens (Ehr.) was abundant at SW. Trout and NE. Muskellunge but elsewhere it was either present in very small numbers or absent It is classed as a psammoxene by Myers, but more likely it is a psammophile.

Proales minima (Montet) occurred in medium numbers at Plum. In nearly all other beaches it was present in small numbers or rarely. It was not reported by Myers but Wiszniewski found it to be abundant.

Trichocerca intermedia (Stenroos) occurred in 15 beaches, ranging from small numbers to very numerous. It was found back to a distance of 300 cm. and often reached a total of 100 individuals per sample.

Trichocerca tenuior (Gosse) was found in all beaches except Michigan and Superior. Although it was abundant in some beaches, medium numbers were found in most instances.

Trichocerca tigris (Müller) was found scattered in small numbers in seven of the beaches.

Although considerable variation was found, little significance can be attached to the numbers of psammophile species found in individual beaches (see Table 20). This is due largely to the fact that some beaches were studied less intensively than others. Obviously, the more carefully a beach was studied, the more chance there was of finding some of the less abundant forms. Poor environmental conditions, however, are no doubt responsible

for the few psammophile rotifers encountered at Superior, Michigan, and Monona, where only six, seven, and nine species were recorded, respectively. At the other extreme, 20 or more species were found at Mendota, N. Trout, S. Trout, E. White Sand, and NE. Muskellunge beaches. From ten to 18 species were encountered at the other 12 locations.

Psammobiotic species

The following species from Wisconsin beaches were found to be confined almost exclusively to the exposed sand.

Cephalodella compacta Wisz. was scattered evenly in the hygropsammon and eupsammon in nearly all of the beaches. The numbers ranged from rare to medium. A few samples contained more than 20 individuals.

Dicranophorus hercules Wisz. is a very characteristic psammobiotic species which was found scattered evenly between the water's edge and the 300 cm. stations. The majority of the specimens were of the variety *typica* but v. *capucinoides* and individuals intermediate between these two forms were common in some instances. Only in a few cases, however, were as many as ten members of this species found in single samples.

Elosa spinifera Wisz. was found in five beaches and in every case less than five specimens per series of samples were found. Wiszniewski found it to be abundant in the Polish beaches.

Encentrum diglandula (Zawadowsky) was rare at Mendota and N. Trout and absent from all of the other beaches. In the Polish beaches it was quite abundant.

Encentrum insolitum Myers was abundant in the hygropsammon at Michigan in the spring when as many as 30 individuals per sample were found. A few were found also at N. Trout, Superior, E. White Sand, and Muskellunge beaches. Myers states that this form is a winter species.

Euchlanis arenosa Myers was found in small to medium numbers in 11 beaches, usually within 50 cm. of the water's edge where the sand was saturated. A few specimens were also found in the submerged sand near the water's edge.

Lecane inquieta Myers was present in 11 of the 20 beaches studied. In contrast to the situation found by Myers, this species was confined almost exclusively to the eupsammon, seldom being found as close to the water as 50 cm. Some samples as far back as the 300 cm. stations contained more than 200 specimens.

Lecane mucronata Myers occurred only in the hygropsammon of lakes having acid waters—Pallette, Weber, Starrett, Day, and Crystal. The numbers varied from rare to common, with more than 15 specimens being found in a few samples. Like *Euchlanis arenosa,* a few specimens of this species were found in the submerged sand.

TABLE 21. RELATIVE ABUNDANCE OF PSAMMOBIOTIC ROTATORIA
1 = very abundant, 2 = numerous, 3 = medium numbers, 4 = small numbers, 5 = rare.

Beach	*Cephalodella compacta*	*Dicranophorus hercules*	*Elosa spinifera*	*Encentrum diglandula*	*E. insolitum*	*Euchlanis arenosa*	*Lecane inquieta*	*L. mucronata*	*L. paraclosterocerca*	*L. psammophila*	*Lindia janickii*	*Myersinella tetraglena*	*Trichocerca insolens*	*Wierzejskiella* spp.	Total number of species
Monona	....	5	....	....	....	....	....	....	....	....	....	....	....	4	2
Mendota	4	3	4	5	4	....	....	....	4	....	....	5	....	4	8
Arbor Vitae	....	4	....	....	....	....	2	....	4	....	....	....	....	....	3
Plum	4	4	....	....	....	....	3	....	3	....	....	....	3	3	6
N. Trout	3	3	4	5	5	3	4	....	3	5	....	4	4	3	12
S. Trout	3	4	5	....	....	3	5	....	3	....	....	3	4	3	9
SW. Trout	....	4	....	....	....	3	....	....	2	....	4	5	4	4	7
Michigan	....	3	....	....	3	....	....	....	....	....	....	....	....	2	3
Superior	....	4	....	....	5	....	....	....	....	....	....	....	3	3	4
E. White Sand	3	4	5	....	4	4	4	....	2	....	5	5	....	4	10
NE. White Sand	4	4	....	....	....	4	1	....	1	5	....	....	....	4	7
Boulder	4	4	....	....	....	4	4	....	4	....	4	3	3	5	9
NE. Muskellunge	4	4	4	....	5	4	....	....	1	5	....	4	3	4	10
E. Muskellunge	5	3	....	....	5	3	....	....	1	5	....	4	4	3	9
Pallette	4	4	....	....	....	3	2	4	2	....	....	4	4	3	9
Weber	4	4	....	....	....	....	....	5	2	....	....	....	4	....	5
Starrett	4	3	....	....	....	3	3	3	2	....	4	....	2	3	9
Day	3	4	....	....	....	....	2	3	2	....	....	....	....	....	5
W. Crystal	5	5	....	....	....	....	....	3	3	....	....	....	4	....	5
E. Crystal	4	4	....	....	....	3	2	4	3	5	....	....	3	3	9

Lecane paraclosterocerca Pennak was found to be the most abundant psammobiotic form and was absent only at Monona, Michigan, and Superior. In eight of the beaches it was the predominant species. Many samples contained more than 400 specimens. The distribution has been briefly discussed by Pennak (1939).

Lecane psammophila Wisz. was rarely found in five of the beaches and was not found in any of the other 15. Myers also recorded it as being rare, but Wiszniewski found that it was one of the principal constituents of the Polish psammolittoral.

Lindia janickii Wisz. occurred in small numbers in four beaches.

Myersinella tetraglena (Wisz.) was present in nine beaches. Medium numbers were found at S. Trout and Boulder but fewer elsewhere. This species was confined almost exclusively to the eupsammon where a few samples contained more than 10 individuals.

Trichocerca insolens Myers was found in 13 beaches, usually within 100 cm. of the water's edge. The numbers ranged from few to abundant.

Wierzejskiella sabulosa Wisz. occurred in most of the beaches but always in small numbers, seldom more than three per series of samples.

Wierzejskiella velox Wisz. was found in varying numbers in all but four of the beaches. It was scattered between the water's edge and some of the

350 cm. stations. Occasionally as many as 30 specimens were found in individual samples.

As in the case with the psammophile Rotatoria, no definite conclusions can be drawn concerning the numbers of psammobiotic species found in individual beaches due to the fact that certain beaches were studied more intensively than others. It is to be noted, however, (see tables 20 and 21) that the larger numbers of psammobiotics were commonly found in those beaches which had the larger numbers of psammophiles. This is true for N. Trout, S. Trout, E. White Sand, and NE. Muskellunge. Similarly, small numbers of both psammobiotics and psammophiles were characteristic of Monona, Arbor Vitae, Michigan, and Superior beaches.

In both of the foregoing lists it will be noted that there are pronounced differences in the relative abundance of some of the species reported from New Jersey, Poland, and Wisconsin, including the addition of six species from Wisconsin which are previously unreported from sandy beaches. The following psammophile species were listed as common to abundant by either Wiszniewski or Myers, but have not been found in the Wisconsin beaches:

Cephalodella tenuior (Gosse)
Dicranophorus artamus Harring and Myers
Dicranophorus capucinus Harring and Myers
Dicranophorus rostratus (Dixon-Nuttal and Freeman)
Encentrum arvicola Wulfert
Gastropus minor (Rousselet)
Lecane levistyla (Olofsson)
Notommata tripus Ehr.
Taphrocampa annulosa Gosse
Trichocerca uncinata (Voigt)
Trichocerca tortuosa (Myers)

Myers has stated that the number of psammophile species found in the hygropsammon is dependent upon the proximity of the submerged aquatic vegetation, there being larger numbers where the vegetation (especially those species having finely divided leaves) is close to the shore. In the present study the beach at SW. Trout had the largest amount of submerged aquatic vegetation adjacent to the water's edge, but the number of psammophile species found was no greater than at some of the beaches having very little aquatic vegetation. Nor were especially large numbers of species found at Plum, Starrett, and Day beaches where quantities of marginal vegetation were also present.

Seven psammobiotic species were reported as being common to abundant by Wiszniewski or Myers, but were not encountered in Wisconsin:

Aspelta egregia Myers
Lecane mitella (Myers)
Lecane tenua Myers
Trichocerca pygocera (Wisz.)
Trichocerca taurocephala (Hauer)

Trichotria eukosmeta Myers
Wigrella depressa Wisz.

GENERAL DISTRIBUTION

In most instances the great majority of the Rotatoria were found in the top 3 cm. of sand between the water's edge and the 250 cm. stations. The range of numbers was extreme; some 10 cc. sand samples taken from the surface of the sand within 150 cm. of the water's edge contained only five or ten specimens, sometimes fewer; other samples taken from corresponding regions of certain beaches contained hundreds, and, in a few instances, thousands of specimens. This variety of population is shown in Table 22 where the data for one series of samples from each of seven different beaches are given.

According to the data presented in Table 23, the beaches may be roughly divided into three categories on the basis of mean numbers of Rotatoria per 10 cc. of sand (calculated for the uppermost 4 cm.). Those beaches which had mean populations of less than 20 rotifers per sample may be considered to have small populations; these were W. Crystal, Boulder, Superior, Mendota, Monona, and SW. Trout (two series only). Monona and Mendota are not strictly comparable with the others because samples were taken there during spring and fall; summer collections would undoubtedly show larger populations. Both Boulder and W. Crystal are very narrow and consequently the larger numbers usually found between 100 and 200 cm. from the water's edge in wider beaches have no chance to appear. In the second category may be placed all beaches having medium populations—between 20 and 40 rotifers per sample; these beaches were Plum, N. Trout, Michigan, E. White Sand, E. Muskellunge, and E. Crystal. The other beaches all had mean populations of more than 40 rotifers per sample. Exclusive of SW. Trout, the highest was 83.4 at NE. White Sand. S. Trout was second highest with 62.2.

Low temperatures and poor food supply at Superior may well be responsible for the small numbers of rotifers found in those sands. In midsummer, when the samples were collected, the lake water temperature was only 5.0°C., and since much of the sand is washed almost continuously by wave action it is safe to conclude that the beach temperature does not rise much above this reading. Particulate dead organic matter was almost negligible and only a very few algal cells were found in this beach.

Nevertheless, even a small amount of organic material may be sufficient to support large numbers of Rotatoria. Although E. Crystal, for example, contained only about 1.0 mg. of organic matter per 10 cc. of sand, the populations for the four series collected there ranged between 15.7 and 40.6 per sample. Indeed, several single samples contained more than 100 rotifers with one containing 370. Weber and NE. Muskellunge also had large numbers but contained only 2.0 and 1.1 mg. of organic matter per 10 cc. of sand, respectively. In spite of the fact that Michigan contained only 0.6 mg. of

TABLE 22. DISTRIBUTION OF ROTATORIA IN SEVEN TYPICAL SERIES OF 10 CC. SAND SAMPLES

Distances from water's edge (stations) indicated horizontally in cm. Eight successive samples, each one cm. in thickness, taken between the surface of the sand and a depth of eight cm. at each station. Results expressed as number of Rotatoria per 10 cc. sand sample. Psammobiotic and psammophile rotifers only.

Distance from water's edge, cm.

Beach and date	Depth of sample, cm.	0	50	100	150	200	250
Monona Oct. 29, 1937	1	10	60	156	40	36	...
	2	6	...	...	7	...	1
	3	..	...	3	...	3	...
	4	..	...	...	...	...	...
	5	..	...	...	...	...	...
	6	..	...	...	...	...	...
	7	..	...	...	...	...	...
	8	..	...	...	...	...	...

Beach and date	Depth of sample, cm.	0	50	100	150	200	250	300	350
N. Trout Aug. 1, 1937	1	4	24	85	196	294	90	97	...
	2	5	24	6	22	15	2	3	8
	3	6	37	3	...	4	...	1	1
	4	13	33	...	1	...	...	6	...
	5	5	4	...	...	...	...	2	...
	6	7	4	...	...	...	...	...	...
	7	10	4	...	...	...	...	...	...
	8	3	1	...	...	...	...	...	...

Beach and date	Depth of sample, cm.	0	25	50	75	100	125
SW. Trout July 19, 1936	1	46	518	411	4060	11550	2055
	2	5	14	19	92	2430	1820
	3	1	16	12	20	1410	5070
	4	..	6	3	8	238	970
	5	..	...	...	3	351	7
	6	..	...	...	...	59	3
	7	..	...	...	...	8	...
	8	..	...	...	...	...	...

Beach and date	Depth of sample, cm.	0	50	100	150	200	250	300
Michigan May 29, 1937	1	12	14	1	48	32	8	4
	2	42	13	14	26	32	35	...
	3	67	36	12	42	23	12	...
	4	102	33	18	8	4	7	...
	5	88	35	21	5	9	2	...
	6	154	16	12	6	4	3	...
	7	72	54	5	...	...	...	...
	8	101	23	13	...	...	...	...

Beach and date	Depth of sample, cm.	0	100	200	260	320
Superior Aug. 8, 1937	1	5	...	...	...	...
	2	2	...	...	...	...
	3	5	...	...	...	...
	4	6	2	...	...	...
	5	1	5	1	...	...
	6	4	7	...	...	...
	7	1	...	...	...	...
	8	3	...	...	...	...

Beach and date	Depth of sample, cm.	0	50	100	150	200	250	300
Pallette July 11, 1937	1	399	738	1128	845	16	...	...
	2	120	52	22	51	2	...	...
	3	22	11	4	38	...	1	...
	4	17	2	...	1	5	...	2
	5	10	...	1	...	...	2	...
	6	9	...	...	...	1	...	1
	7	8	...	...	...	...	...	...
	8	2	...	...	...	...	...	...

Beach and date	Depth of sample, cm.	0	50	100	150	200	250	300
E. Crystal July 8, 1937	1	13	34	47	140	370	69	6
	2	127	11	4	81	102	19	...
	3	31	...	...	4	42	2	...
	4	5	...	...	...	20	...	...
	5	1	...	...	...	5	1	...
	6	..	...	...	...	2	...	...
	7	..	...	...	...	...	...	...
	8	..	...	...	...	...	...	...

TABLE 23. MEAN NUMBERS OF ROTATORIA (PSAMMOPHILE AND PSAMMOBIOTIC SPECIES) PER 10 CC. OF SAND FOR 66 DIFFERENT SERIES OF SAMPLES
Calculated for top 4 cm. of sand only.

Beach	Date	Rotatoria per 10 cc. of sand
Monona	June 28, 1937	7.8
	Sept. 8, "	10.2
	Oct. 29, "	13.4
Mendota	May 18, 1936	6.3
	Sept. 1, "	1.6
	Nov. 12, "	0.0
	Apr. 16, 1937	.1
	May 7, "	.4
	May 14, "	2.0
	May 28, "	8.0
	June 4, "	30.4
	June 22, "	17.0
	Sept. 3, "	6.0
	Oct. 8, "	11.9
Arbor Vitae	Aug. 5, 1936	44.5
Plum	July 22, 1936	18.4
	Aug. 19, 1938	22.1
N. Trout	July 5, 1936	46.0
	Aug. 16, "	19.2
	July 4, 1937	19.2
	July 18, "	19.2
	Aug. 1, "	30.3
	Aug. 17, "	17.3
	July 3, 1938	25.2
	July 31, "	6.8
	Aug. 4, "	12.2
	Aug. 26, "	20.0
S. Trout	July 19, 1936	146.6
	Aug. 13, "	45.5
	July 5, 1937	118.5
	Aug. 15, "	37.0
	July 12, 1938	15.8
	Aug. 15, "	10.0
SW. Trout	July 19, 1936	1200.0
	Aug. 13, "	12.6
	July 23, 1937	20.0

Beach	Date	Rotatoria per 10 cc. of sand
Michigan	May 29, 1937	23.1
Superior	Aug. 18, 1937	1.0
	July 17, 1938	3.0
E. White Sand	July 22, 1936	19.4
	July 18, 1937	38.7
	July 24, 1938	50.6
NE. White Sand	Aug. 18, 1938	83.4
Boulder	Aug. 2, 1936	7.5
	Aug. 14, 1937	5.2
	July 24, 1938	12.6
NE. Muskellunge	July 16, 1936	5.9
	Aug. 21, "	12.7
	July 13, 1937	135.6
	Aug. 22, "	42.3
E. Muskellunge	July 31, 1938	59.4
	Aug. 13, "	13.2
Pallette	July 30, 1936	28.0
	July 11, 1937	124.1
	July 10, 1938	17.3
Weber	July 29, 1936	36.1
	Aug. 11, "	48.7
Starrett	July 30, 1937	88.2
	Aug. 7, 1938	23.4
Day	Aug. 2, 1936	34.6
	July 27, 1937	51.4
W. Crystal	July 9, 1936	15.3
E. Crystal	July 9, 1936	15.7
	July 8, 1937	40.6
	July 3, 1938	29.0
	Aug. 23, "	33.0

organic matter per sample, a population of 23.0 rotifers per sample was found. The great majority of these specimens were *Encentrum insolitum* and *Wierzejskiella velox*, both abundant during the spring. Conditions later in the year are not known.

Certainly, in this study, there is no correlation between numbers of Rotatoria and organic matter. Monona, Mendota, N. Trout, S. Trout, and Starrett all contained high quantities of organic material—more than 5 mg. per sample, but these beaches had mean populations which ranged from 10.5 to 62.2 rotifers per sample.

In some of the beaches great variations in the numbers were found from time to time. The greatest variation was found at SW. Trout. On July 19, 1936 a very dense population of rotifers was found, the mean population being 1200.0 per sample. Less than a month later, however, the numbers had dropped to 12.6 per sample in approximately the same area of the beach. In the former series (see Table 22) an enormous population occurred at the 75, 100, and 125 cm. stations. Seven samples contained more than 1000 specimens and the surface sample at the 100 cm. station contained 11,550, by far

the most concentrated condition found during this study. This is equivalent to about 3,610,000 rotifers per liter of water. The great majority of the specimens were the following species: *Lepadella patella, Lecane hamata, Lecane paraclosterocerca, Lecane inermis, Lecane nana, Lecane verecunda.* This series was the only one which contained large numbers of the last three mentioned species, which were otherwise rare. It is significant that the sand in which such large numbers were found contained a rich culture of Oscillatoria. Although this alga was found in practically all collections, it was abundant in this instance only. The two later collections made at SW. Trout contained very few specimens of *Lecane inermis, Lecane nana,* and *Lecane verecunda.* Other less striking variations are as follows: NE. Muskellunge, a 23-fold variation, from 5.9 to 135.6 rotifers per sample; S. Trout (six series), a 15-fold variation, from 10 to 146.6 specimens; Pallette and N. Trout both had 7-fold variations.

In most instances pronounced variations within a beach were due to increases or decreases in the numbers of all species, but in some cases large "crops" of a single species dominated all the others. *Lecane hamata* most frequently caused these conditions. The maximum population of 46.0 per sample at N. Trout on July 5, 1936, as well as the means of 146.6 and 118.5 at S. Trout were due chiefly to large numbers of this form. The greatest population found at Pallette, 124.1 per sample, was due to large numbers of both *Lecane hamata* and *Lecane paraclosterocerca,* while the mean of 135.6 at NE. Muskellunge on July 13, 1937, was due almost entirely to hundreds of specimens of *Lecane paraclosterocerca.* Many less striking examples could be cited.

One of the factors which might be immediately suspected as causing decreases in the rotifer populations is the effect of heavy wave action which might serve to wash these organisms out of the sand and back into the lake. So far as the 10 series collected at N. Trout are concerned, there is some evidence for such action. During one or two days previous to the collection of seven of the series there were prevailing onshore winds ranging from fresh to very strong; sometimes the waves reached the 300 cm. station. These seven series all contained comparatively small populations, ranging from 6.8 to 20.0 per sample. The other three series were collected after four or five days of little wave action and had mean populations ranging from 25.2 to 46.0 per sample. The heavy wash at Superior is probably even more restrictive than the low temperatures and poor food supply. We do not have sufficient data from any of the other beaches to justify further conclusions. It is interesting to note, however, that S. Trout, which is quite similar to N. Trout except that it is exposed to little wave action, had considerable variations in numbers and about twice as many rotifers as N. Trout. Day, Starrett, E. Muskellunge, and SW. Trout are also very little washed by waves but had pronounced variations. Certainly wave action must be only a single

TABLE 24. SUMMARY OF DISTRIBUTION OF ROTATORIA; 66 SERIES OF SAMPLES

Distance from water's edge indicated horizontally in cm. Each value represents the total number of psammophile and psammobiotic rotifers found in the eight successive 10 cc. sand samples, each one cm. in thickness, between the surface of the sand and a depth of 8 cm. Results have been interpolated in some instances where stations were not established at 50 cm. intervals.

Beach	Date	Distance from water's edge, cm.								
		—50	0	50	100	150	200	250	300	350
Monona	June 28, 1937	2	84	35	34	3	0	...	...	...
	Sept. 8, "	...	53	6	2	67	97	19	...	...
	Oct. 29, "	...	19	60	157	47	37	1	...	...
Mendota	May 18, 1936	...	14	100	9	74	39	8	...	...
	Sept. 1, "	...	0	7	5	3	18	...	...	...
	Nov. 12, "	...	0	0	1	0	0	...	...	...
	Apr. 16, 1937	...	2	2	1	0	0	0	...	...
	May 7, "	...	0	5	8	0	0	...	...	...
	May 14, "	...	2	9	3	54	0	0	...	...
	May 28, "	...	131	10	10	79	26	3	...	...
	June 4, "	...	289	245	36	223	73	45	...	...
	June 22, "	22	37	222	117	41	47	54	...	...
	Sept. 3, "	...	12	18	110	32	1	0	...	...
	Oct. 8, "	...	3	0	15	37	246	26	16	...
Arbor Vitae	Aug. 5, 1936	...	117	206	101	374	...	...	...	...
Plum	July 22, 1936	...	126	28	92	...	...	...	...	...
	Aug. 19, 1938	0	253	43	2	...	...	...	...	...
N. Trout	July 5, 1936	...	116	133	250	262	...	...	...	...
	Aug. 16, "	...	7	50	146	169	27	0	...	...
	July 4, 1937	9	64	195	63	122	102	65	45	...
	July 18, "	...	67	87	108	132	23	8	0	...
	Aug. 1, "	...	53	130	94	219	313	92	109	9
	Aug. 17, "	...	44	33	35	86	49	146	62	9
	July 3, 1938	...	66	56	215	119	107	...	...	...
	July 31, "	...	0	11	65	31	44	...	...	...
	Aug. 4, "	0	2	5	20	62	168	...	...	...
	Aug. 26, "	1	65	110	106	87	85	52	...	...
S. Trout	July 19, 1936	...	200	512	284	831	985	...	...	...
	Aug. 13, "	...	94	140	199	120	235	183	110	...
	July 5, 1937	...	1043	1009	638	355	261	49	3	...
	Aug. 15, "	...	177	308	66	61	59	350	18	...
	July 12, 1938	6	33	97	37	162	9	...	...	...
	Aug. 15, "	4	50	44	69	35	2	...	...	...
SW. Trout	July 19, 1936	...	52	445	16046	...	...	...	...	...
	Aug. 13, "	...	23	32	125	...	...	...	...	...
	July 23, 1937	...	219	129	34	58	26	...	...	...
Michigan	May 29, 1937	...	638	224	96	135	105	57	4	...
Superior	Aug. 8, 1937	...	27	...	14	...	1	0	0	0
	July 17, 1938	1	37	7	20	16	15	3	...	...
E. White Sand	July 22, 1936	...	25	100	81	...	...	...	...	...
	July 18, 1937	...	70	119	250	285	430	80	5	4
	July 24, 1938	...	166	195	95	764	210	107	20	...
NE. White Sand	Aug. 18, 1938	...	103	676	959	185	43	129	...	...
Boulder	Aug. 2, 1936	...	50	26	2	...	...	...	...	...
	Aug. 14, 1937	...	37	5	...	...	...	...	...	...
	July 24, 1938	21	82	82	56	6	...	...	...	...
NE. Muskellunge	July 16, 1936	4	55	17	27	6	...	...	...	...
	Aug. 21, "	...	279	120	127	139	184	39	...	...
	July 13, 1937	...	910	487	875	638	...	...	...	...
	Aug. 22, "	...	94	452	449	119	30	28	11	...
E. Muskellunge	July 31, 1938	0	32	1194	62	0	0	...	...	...
	Aug. 13, "	4	101	61	100	2	0	0	...	...
Pallette	July 31, 1936	...	44	239	65	99	27	...	...	...
	July 11, 1937	...	587	803	1155	935	24	3	3	...
	July 10, 1938	27	62	60	25	58	161	...	...	...
Weber	July 29, 1936	...	69	215	71	...	...	...	...	...
	Aug. 11, "	...	343	376	155	158	44	...	...	...
Starrett	July 30, 1937	...	725	193	228	528	96	...	...	...
	Aug. 7, 1938	46	186	276	5	0	0	...	...	...
Day	Aug. 2, 1936	...	54	104	64	...	...	...	...	...
	July 27, 1937	...	103	79	130	843	74	7	...	...
W. Crystal	July 9, 1936	...	199	21	...	...	...	...	...	...
E. Crystal	July 9, 1936	...	121	97	88	14	5	...	...	...
	July 8, 1937	...	177	45	51	125	441	91	6	...
	July 3, 1938	6	94	95	96	138	326	3	...	...
	Aug. 23, "	43	422	235	35	0	0	0	...	...

one of a complex linkage of environmental factors affecting numbers. Nevertheless, from the standpoint of this study, there are no apparent constant correlations between numbers of rotifers and such factors as sand grain size, dissolved carbon dioxide, dissolved oxygen, pH, and residues of the capillary water.

The eight series of samples taken at Mendota in 1937 demonstrate the appearance and abundance of the psammolittoral rotifers in the spring. On April 16 only one specimen was found; on May 7, 19 were found; a week

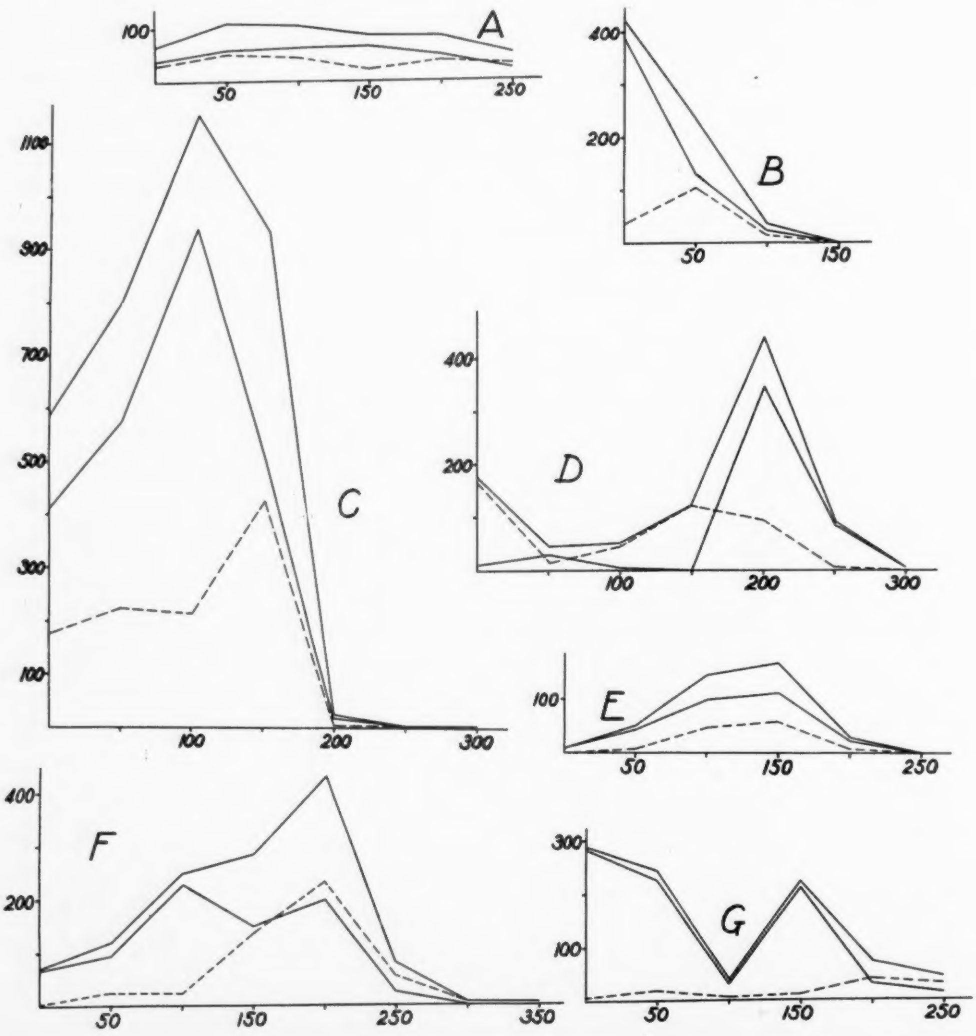


FIG. 11. Horizontal distribution of Rotatoria in seven typical series of samples. Distances from water's edge indicated in cm. as abscissae. Numbers of rotifers per 80 cc. of sand, between the surface and a depth of 8 cm., indicated as ordinates. Broken-line curves indicate psammobiotic rotifers; lower solid curves indicate psammophile rotifers; uppermost curves indicate total rotifers. A = N. Trout, Aug. 26, 1938; B = E. Crystal, Aug. 23, 1938; C = Pallette, July 11, 1937; D = E. Crystal, July 8, 1937; E = N. Trout, Aug. 16, 1936; F = E. White Sand, July 18, 1937; G = Mendota, June 4, 1937.

later the mean population was 2.0 per sample, and by May 28 an average of 8.0 per sample was found. A maximum of 30.4 occurred on June 4, but by June 22 it had decreased to 17.0. During the fall, 6.0 and 11.9 per sample were found on September 3 and October 8, respectively. The results of the three series in 1936 fit in fairly well with these data. By November 12, 1936, the rotifers had disappeared from the sand entirely.

Wiszniewski (1934a) indicates that the psammolittoral rotifers of Poland appear in April and disappear in November. Two maxima are given, one in June and one in late September with a summer minimum in August.

HORIZONTAL DISTRIBUTION

In general, most of the Rotatoria were confined to the 250 cm. of sand immediately adjacent to the water's edge, but, on account of changing physical, chemical, and biological conditions in the sand, as well as localized "crops" of certain species, many different types of horizontal distributions were found within that distance. Some of these are shown in Figures 11 and 12. The former figure gives the results for seven series of sand samples which contained greater populations of psammophile than psammobiotic species. In a few cases a small comparatively homogeneous population was found over most of the width of the beach. This is shown for N. Trout on August 26, 1938, when the total numbers of Rotatoria ranged from 52 at the 250 cm. station to 110 at the 50 cm. station. In the majority of instances, however, pronounced maxima were found, ranging up to more than 1100 per station. These maxima, due mainly to the preponderance of psammophiles, were found anywhere between the water's edge and the 200 cm. stations.

Figure 12 shows four collections in which psammobiotic rotifers predominated. Like the psammophiles, this group was found in maximum abundance at various locations between the water's edge and the 200 cm. stations. In several instances the psammobiotics totaled more than 600 individuals per station.

The mean horizontal distribution for all series is shown in Figure 13. Each value represents the mean number of Rotatoria for the eight successive 10 cc. sand samples taken between the surface and a depth of 8 cm. The maximum number of psammobiotic forms was 82 at the 150 cm. station, and the second highest was 59 at the 50 cm. station, while the 0 cm. station was slightly lower with 53. Beyond the 150 cm. station the numbers gradually decreased to two at 350 cm. Psammophile forms were more numerous than the psammobiotics at all stations except at 250 cm. Between the water's edge and the 150 cm. station a range of 95 to 110 psammophiles per station was found. Beyond, there was a gradual decrease to four at the 350 cm. station. As to total Rotatoria, a maximum of 179 per station was found for the 150 cm. station, although 169 were at the 150 cm. station and 150 at the water's edge. These results are not to be interpreted as being typical, since

summer collections at most beaches would give much larger numbers than are indicated. The calculated means are particularly low because of the inclusion of spring and fall collections, when very few rotifers were found, as well as data from such poor collecting grounds as the beach at Superior.

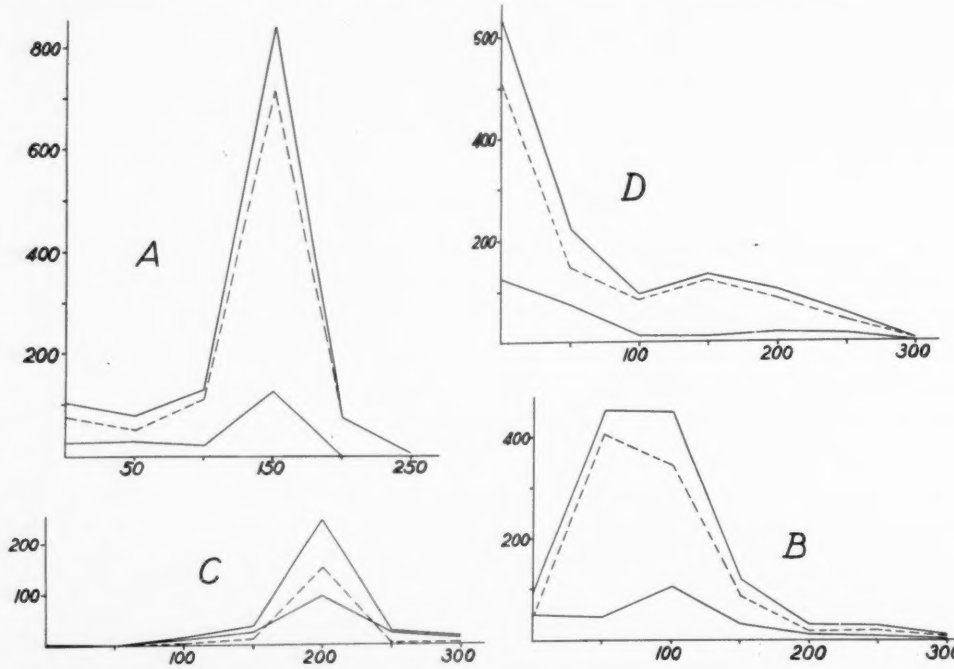


Fig. 12. Horizontal distribution of Rotatoria in four typical series of samples. A = Day, July 27, 1937; B = NE. Muskellunge, Aug. 22, 1937; C = Mendota, Oct. 8, 1937; D = Michigan, May 29, 1937. See legend of Figure 11 for other data.

These figures differ slightly from those of Pennak (1939b) who showed that there were larger numbers of psammobiotics than psammophiles at the 150 cm. station. The addition of data gathered during 1938, however, has changed the relationships of the curves somewhat.

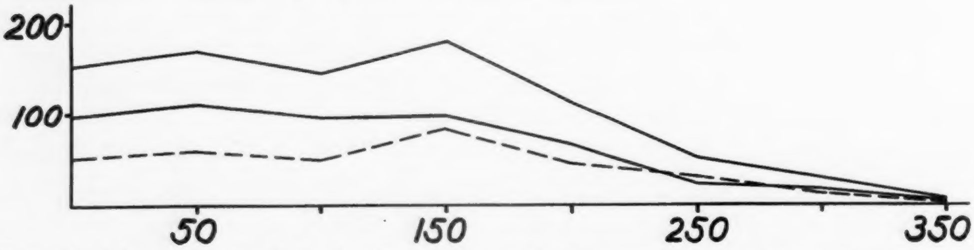


FIG. 13. Mean horizontal distribution of Rotatoria, all samples. See legend of Figure 11 for other data.

In view of the fact that Rotatoria are customarily regarded as true aquatic organisms, the occurrence of large numbers in the thin surface films around the sand grains as far as 300 cm. from the lake's edge seems paradoxical. Their presence in the sand at the water's edge under conditions of complete saturation as well as in the sand 250 or 300 cm. from the water's edge where

there is very little water shows the great tolerance of this group. In some cases in outer beaches the water content of the surface layers was so low that no rotifers were found there, but were confined to the deeper layers. This was found at the 230 and 270 cm. stations in two series at Mendota, where the top 3 cm. contained only a few stragglers, but the sand 4 to 8 cm. deep contained a fair population.

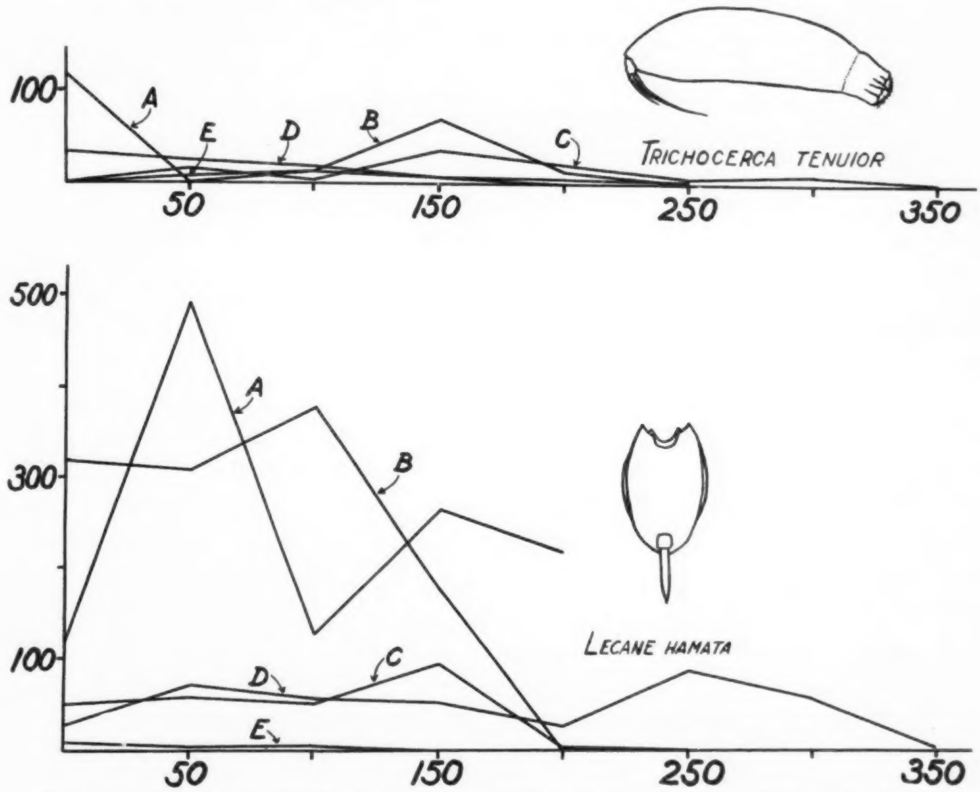


FIG. 14. Horizontal distribution of two species of psammophile Rotatoria. Distance from water's edge indicated horizontally in cm. Ordinates represent numbers of rotifers per eight 10 cc. sand samples, taken between the surface of the sand and a depth of 8 cm. Each curve represents the results of one series of samples. Curves for *Trichocerca tenuior* as follows: A = Starrett, B and C = N. Trout, D = Pallette, E = NE. Muskellunge. Curves for *Lecane hamata:* A = S. Trout, B = Pallette, C and D = N. Trout, E = Starrett.

A considerable number of samples taken from the submerged sand 30 to 50 cm. from the water's edge has demonstrated that this region (hydropsammon) is a very poor collecting ground for rotifers. In comparison with the numbers found at the 0 cm. stations, the submerged sand contained only 19.7% as many.

HORIZONTAL DISTRIBUTION OF INDIVIDUAL SPECIES

The peculiarities of horizontal distribution of a number of species, already mentioned in the species lists, are indicated more precisely in Figures 14 and 15. In the former figure the distribution of two psammophile forms

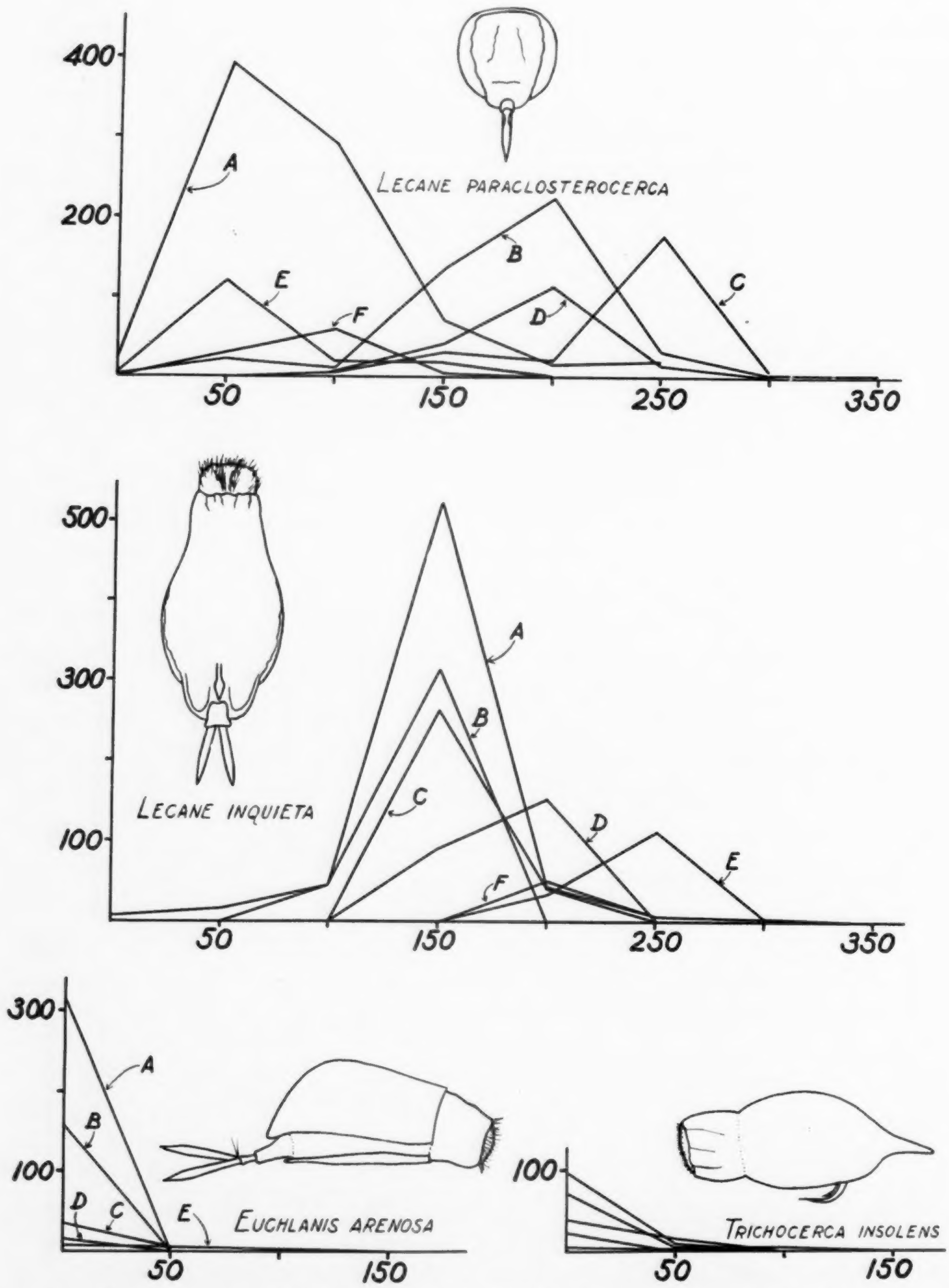


FIG. 15. Horizontal distribution of four species of psammobiotic Rotatoria. Curves for *Lecane paraclosterocerca:* A = NE. Muskellunge, B = E. White Sand, C and D = N. Trout, E = Pallette, F = E. Crystal. *Lecane inquieta:* A = Day, B = Pallette, C = Starrett, D and F = E. Crystal, E = N. Trout. *Euchlanis arenosa:* A = S. Trout, B = Pallette, C and E = N. Trout, D = E. White Sand. *Trichocerca insolens:* curves shown for five typical series of samples, various beaches. See legend of Fig. 14 for other data.

is shown. *Trichocerca tenuior,* although common, was rarely found in large numbers but was distributed as far back as 350 cm. from the water's edge. *Lecane hamata* also was found over the entire widths of beaches, sometimes in very small numbers, sometimes in quantities of more than 500 per station.

Among the psammobiotic species (Fig. 15) *Lecane paraclosterocerca* was found in a wide population range over the entire widths of the beaches; it is significant, however, that very few occurred at the 0 cm. stations. *Lecane inquieta* was confined, for the most part, to the middle and outer regions of the beaches where the sand was only partially saturated. Both *Euchlanis arenosa* and *Trichocerca insolens* on the other hand, were confined to the saturated sand near the water's edge. In several instances more than 300 were found at the 0 cm. stations. Very few occurred beyond 50 cm.

VERTICAL DISTRIBUTION

The concentration of the Rotatoria in the surface of the sand was even more pronounced than in the cases of the Copepoda and Tardigrada. Of the 21 diagrams shown in Figure 16, SW. Trout on July 19, 1936 had by far the greatest average population for the top cm. of sand with 2773, while Pallette (1937) was second highest with 447. Arbor Vitae, S. Trout, E. White Sand, NE. Muskellunge (1937), Weber, and Starrett were also high with from 123 to 316 rotifers per surface sample. Superior had by far the lowest population with less than one specimen per surface sample and Michigan was second lowest with 17. Monona, Mendota, SW. Trout (excepting July 19, 1936), Boulder, and NE. Muskellunge (in 1936) all had less than 50 per surface sample. In terms of percentages of total numbers, more than 90% of all specimens were confined to the top 2 cm. of sand in the majority of cases. Among the exceptions, Superior had only 17% in the top 2 cm. and Michigan 21%. Mendota, SW. Trout, N. Trout, and Boulder had 69, 76, 81, and 87%, respectively.

Many samples were taken below a depth of 8 cm., but only a very few rotifers were found. On the other hand, considerable numbers in the 8 cm. samples at the 0, 50, and 100 cm. stations at Michigan indicated that many rotifers may have been in deeper layers (see Table 22). In this connection it is interesting to note that in samples taken from the submerged sand, nearly all of the rotifers were found in the top 2 cm.

It is likely that the occurrence of the majority of rotifers in the surface of the sand is a response to greater quantities of dissolved oxygen. This is correlated with the finding of large numbers of rotifers in the deeper layers of sand at the 0 and 50 cm. stations of certain beaches containing little organic material and exposed to waves which continuously bring fresh, oxygenated water to the deeper portions of the sand. Such situations were found at Mendota, N. Trout, Michigan, and Superior. There is little justification for the theory that heavy wave action or severe rains serve to me-

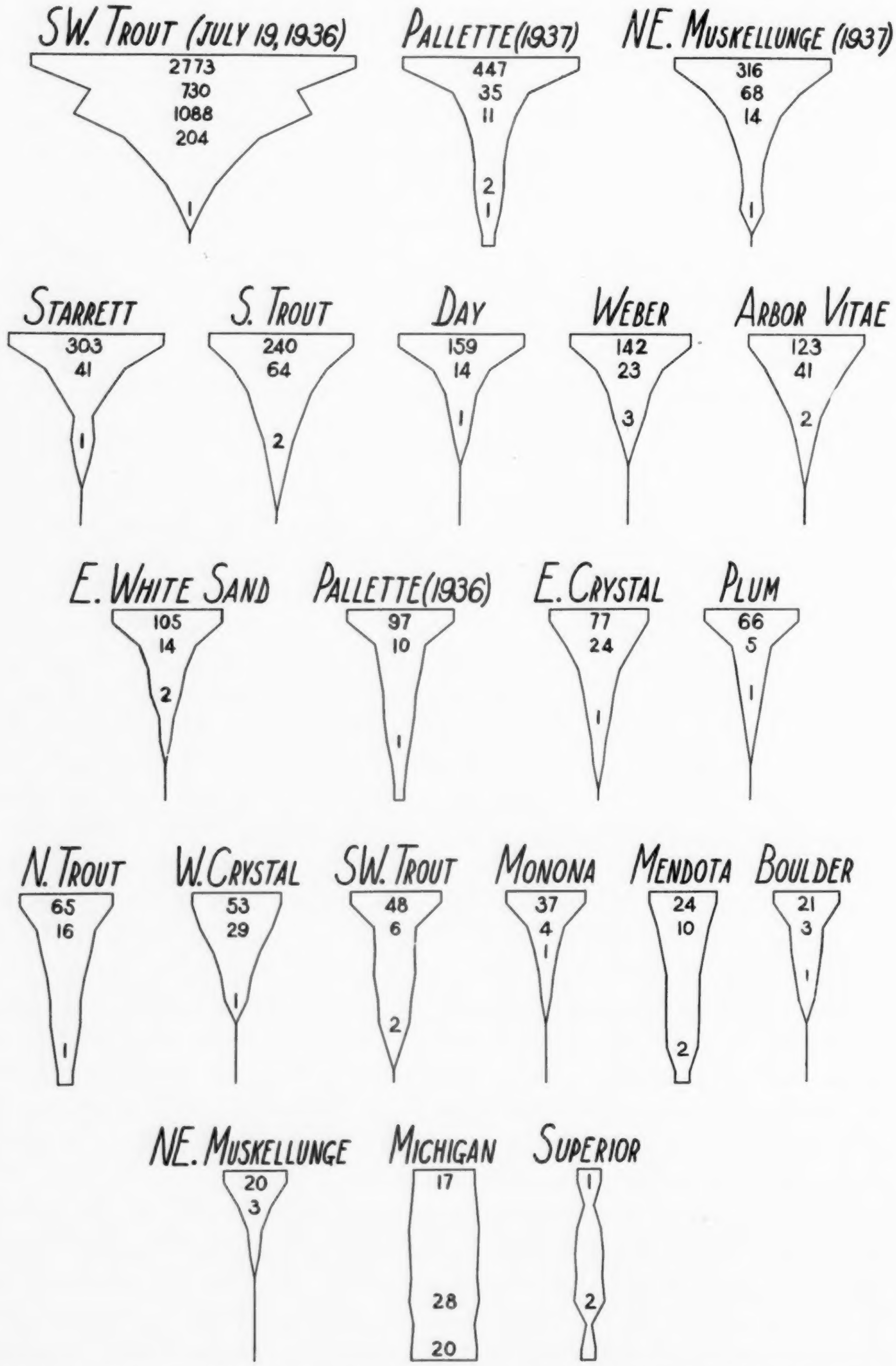


FIG. 16. Mean vertical distribution of Rotatoria, data of 1936 and 1937. Each value represents the mean number of Rotatoria per 10 cc. sand sample for the entire width of each beach.

chanically wash appreciable portions of the rotifer populations into the deeper portions of the sand.

Moreover, there is practically no indication of a differential vertical distribution among the various species. *Euchlanis arenosa* and *Trichocerca insolens,* however, were found almost exclusively in the top cm. of the sand.

OTHER ORGANISMS

BACTERIA

Obviously the sand with its suitable temperatures and constant supply of moisture and organic material forms an ideal substrate for the growth of bacteria. To gain some conception of the numbers of bacteria in the sand, preliminary studies were carried out at the bacteriology laboratory of the Wisconsin Geological and Natural History Survey during the summer of 1938. The results of this work, based chiefly on observations at E. Crystal and N. Trout beaches, have shown that the numbers of bacteria may vary between 33,000 and 8,000,000 per cc. of sand. Furthermore, they were most numerous between 75 and 150 cm. from the water's edge, being 10 to 20 times as abundant there as in the rest of the beach. As is the case with the Rotatoria, 80% to 90% of the bacteria were concentrated in the top 3 cm. of the sand. Of this stratum, the top cm. contained the greatest proportion.

In contrast to the condition obtaining in the lake water, considerable numbers of anaerobes were present in the beaches. The numbers ranged as high as 19,000 per cc. of sand and a common maximum was 5,000. It is thought that improved methods of counting anaerobes, to be used in the future, will show still greater numbers.

PROTOZOA

In most cases the method of washing and preserving destroyed the Protozoa present in the samples. The only reliable evidences were the tests of some of the ameboid forms (Testacea) which withstood the washing operations; Arcella and Centropyxis tests were found scattered in fairly large numbers in some of the samples. In several locations, particularly at soft-water lakes, there were enormous numbers of euglenoids which imparted a greenish cast to the sand. Remains of large ciliates were abundant in some of the samples taken near the water's edge.

The above-mentioned laboratory conducted some work on the Protozoa of the sandy beaches, and like the bacteria, the largest numbers were found between 75 and 150 cm. from the water's edge in the top cm. of the sand. Of the 30 genera found, the small flagellates, both green and colorless, were numerically dominant. Actual numbers ranged from less than 200 to nearly 50,000 per cc. of sand; 7,000 to 9,000 was common.

It was found that strong onshore winds served to wash great numbers of bacteria and Protozoa back into the lake, but within a couple of days

normal numbers were restored. Very little is known concerning the influence of other physical and chemical conditions on the numbers and distribution of bacteria and Protozoa in beaches.

NEMATODA

As would be expected, there were many free-living Nematoda in the sand. No special effort was made to classify the specimens, but a number of individuals selected at random from the samples were found to belong to the genera Trilobus, Actinolaimus, Dorylaimus, and Mononchus. In comparison with some of the other groups, the Nematoda do not require much water. As a consequence, they were found in considerable numbers at some distance from the water's edge. In fact, the maximum numbers were found at the outer edge of the beaches where the sand begins to give way to soil. Except for the Protozoa, the nematodes were the first organisms to appear in the sand in the spring. At N. Trout maximum numbers were found early in July. Mean numbers of these organisms per sample in the various beaches are as follows: SW. Trout, 13.6; N. Trout, 1.9; S. Trout, 1.6; Day, 1.2; Mendota, 1.1. All other beaches contained less than one nematode per sample. None were found at Michigan and Superior.

TURBELLARIA

Turbellarians of the genus Dalyellia were numerous in some locations (up to 15 per sample). By far the great majority were found at the water's edge or within 50 cm. of it. At the 0 cm. stations they were found quite commonly down to a depth of 6 or 8 cm., but farther away from the water they were most likely to be found in the top 2 or 3 cm. of sand. Very few were found more than 100 cm. from the water's edge.

GASTROTRICHA

Gastrotricha were a very common element, being present in most of the samples, particularly those taken within 150 cm. of the water where the sand was quite wet. No special effort was made to count these organisms, but it is known that there were great variations in numbers, from none to over 100 per sample, although the mean for all samples was probably somewhere between 5 and 10.

BDELLOID ROTATORIA

Because of their universal occurrence, the bdelloid rotifers obviously are not characteristic inhabitants of the sand in the same sense that the ploimate Rotatoria are. For this reason, the bdelloids were not tabulated along with the true psammolittoral rotifers. Usually these animals were most abundant in the top 2 cm. of sand, especially where there was much organic material which had not been washed up on the beach too recently. A few samples contained as many as 60 specimens.

OLIGOCHAETA

Naididae of the genera Chaetogaster and Stylaria were usually present in small numbers. SW. Trout, Boulder, and E. White Sand had mean populations of 4.2, 2.7, and 2.3 individuals per sample, respectively. Collections from all other beaches averaged less than 1.2 per sample. The distribution of these animals was sporadic, but the majority was found in the upper 4 cm. of the sand.

INSECTA

Insect larvae (mostly Diptera) were often common, especially during the summer months. The distribution in the sand was random, with no maxima or minima at any particular regions of the beaches. A few were found as deep as 7 or 8 cm. and the great majority was in the upper 4 cm. Although the data are somewhat insufficient, we may say that the larvae were more numerous in beaches having the higher amounts of particulate organic matter. SW. Trout had a mean of over 2 larvae per sample and all other beaches had fewer. None were found at Michigan and Superior.

ALGAE

Many species of plankton algae were found in the sand. The main groups were the Cyanophyceae, Chlorophyceae, and Bacillariae. No counts of numbers were taken but most frequently they were well up into the thousands. It was noticed that the desmids were dominant in the beaches of soft-water lakes and the Cyanophyceae and Bacillariae in beaches of harder lakes. Diatoms at Mendota and N. Trout were found concentrated between the 200 and 250 cm. stations. As would be expected, most of the living algae were confined to the top cm. of the sand where there is sufficient light for photosynthesis.

SUMMARY

This investigation, carried out during the summers of 1936, 1937, and 1938, comprises an ecological study of the microscopic Metazoa (especially the Rotatoria, Tardigrada, and Copepoda) inhabiting the capillary waters of 20 exposed sandy beaches situated on the shores of 15 Wisconsin lakes. Most of the 2702 sand samples were 10 cc. in volume and were collected in layers one cm. in thickness between the surface of the sand and a depth of 8 cm. at varying distances (stations) from the water's edge.

Physical and chemical conditions in the beaches were varied:

(1) Those beaches having considerable slope (8°) had narrow inhabited regions while other beaches having a slope of 3° or 4° contained numbers of organisms as far back as 350 cm. from the water's edge. In an "average" beach the top cm. of sand was found to be 100, 81, 41, and 20% saturated at the water's edge, the 100, 200, and 300 cm. stations, respectively.

(2) In spite of the variety of sands encountered, the interstitial volume was quite uniform, varying between 37 and 43% of the aggregate volume.

(3) Beyond the reach of waves and the effects of capillarity, rain is very important in keeping the sand damp enough to permit the existence of psammolittoral organisms.

(4) On account of the presence of the capillary water and its evaporation, the temperature of the sand is kept down to a degree tolerable to the organisms. Near the water's edge the sand temperatures are governed largely by the lake water temperatures. Only in the drier uninhabited outer portions of the beaches were temperatures of more than 33° recorded.

(5) In some beaches an average of less than 1.0 mg. of particulate organic matter per 10 cc. sand sample was found. At other beaches large amounts occurred; a few individual samples contained more than 50 mg. Windrows of detritus were common on the beaches of the more productive lakes. Near the surface of the sand a portion of the particulate organic material consists of countless living algal cells, which, as a food source, are very likely responsible in some degree for the occurrence of the majority of the microscopic animals in that region of the beach.

(6) Heavy wave action at some of the beaches was responsible for the washing of a considerable portion of the Metazoa (especially the Rotatoria) back into the lake.

(7) The capillary waters were usually more acid than the lake waters. A pH gradient was almost always found between the water's edge and the 100 cm. stations, with the more acid conditions at the distant points.

(8) Dissolved free carbon dioxide also showed a gradient, with an average of 7.1 ppm. in the sand at the water's edge to 18.8 ppm. at the 100 cm. stations. In a few instances more than 30.0 ppm. were found. Wave action serves to prevent the accumulation of free carbon dioxide near the water's edge.

(9) In general, beaches of soft-water lakes contained small amounts of bound carbon dioxide and hard-water lake beaches contained large amounts. Although well-defined gradients were not usual, considerable accumulations of bound carbon dioxide in the sand were common.

(10) Dissolved oxygen was present in smaller quantities in the sand than in the adjacent lake water. A well-defined gradient was found with a mean of 5.5 ppm. in the sand at the water's edge to 0.4 ppm. at the 100 cm. station. In a number of instances many organisms were found in the deeper sand which contained no demonstrable quantities of dissolved oxygen. In spite of this facultative anaerobic tendency, however, the occurrence of the great majority of psammolittoral organisms in the surface layers of the sand is probably related to the availability of oxygen there. Within 50 cm. of the water's edge the waves supply oxygenated water to the sand almost continuously and in this area it was found that the organisms were customarily distributed more deeply than at the distant stations.

(11) Regardless of considerable variation, the capillary waters contained an average of 54% more dissolved inorganic material than the adjacent lake water. Accumulations in soft-water lake beaches were proportionately greater than in other beaches.

(12) The quantities of dissolved organic materials also covered a wide range and were proportionately greater in the soft-water lake beaches. The mean increase over the amount contained in the adjacent lake water was 42%.

The unstability of environmental conditions due to the variable effects of such factors as wave action, temperature, sunshine, bacterial action, dissolved materials, food supply, and beach slope is emphasized. None of the following factors, however, were found to have any constant relationship to either numbers or distribution of the organisms: pH, size of sand grains, dissolved free and bound carbon dioxide, dissolved organic and inorganic materials, and particulate organic matter.

All Tardigrada examined were of the genus Macrobiotus. Some beaches, such as Monona and S. Trout, contained only a few stragglers; others, such as Day and NE. Muskellunge, contained large numbers, up to 300 or 400 in some samples. In general, beaches of soft-water lakes contained the larger populations. Nevertheless, in nearly all of the individual beaches, great variations in numbers were noted from time to time. Horizontally, these organisms were found concentrated in no particular region of the beaches. Large populations might equally well be found near the water's edge, in the middle beaches, or near the outer inhabitable limits of the sand, sometimes 300 cm. from the water's edge. The majority, however, occurred between the 50 and 150 cm. stations. Vertically, 78% of all Tardigrada were confined to the uppermost 3 cm. of the sand. Very few were found as deep as 8 cm.

Three species of harpacticoid Copepoda were found in the exposed sand. Of these, *Parastenocaris brevipes* was present in 19 beaches, *Parastenocaris starretti* occurred at two beaches, and *Phyllognathopus paludosus* was found at only one. As in the case of the Tardigrada, there was a great variation in numbers, from few or none at Monona and Michigan, to over 100 individuals in certain samples at N. Trout and Pallette. Within individual beaches, however, variations were not pronounced from time to time. Slope of the beaches seems to be one of the chief factors in determining the horizontal distribution, apparently due to the amount of capillary water capable of being held in the sand. In beaches having abrupt slopes the copepods were abundant between 50 and 150 or 200 cm. from the water's edge, while in beaches having gradual slopes they were most numerous between 150 and 300 cm. from the water's edge. In the more populous beaches from 60% to 90% of all copepods were found in the top 4 cm. of sand.

Thirty-five psammophile and 15 psammobiotic species of Rotatoria were found. Some forms, such as *Lecane hamata* and *Lecane paraclosterocerca*, were abundant in nearly all beaches; others, such as *Elosa worralli* and *Lecane psammophila*, were found as scattered specimens in two or three beaches. A great range of numbers was found, from a mean of less than 10 rotifers per sample at Boulder and Superior to 83.4 per sample at NE. White Sand. Some individual 10 cc. sand samples contained more than 600. Large variations were found in the rotifer populations of individual beaches due to increases or decreases in the numbers of a single or several species. Due

to localized "crops," many different types of horizontal distributions were found, from a comparatively homogeneous condition to pronounced maxima at various points as far as 250 cm. from the water's edge. Calculations of mean populations show the great majority of the rotifers within 200 cm. of the water's edge and a poorly-defined maximum at 150 cm. A few rotifers were found to be somewhat restricted horizontally. *Trichocerca insolens* and *Euchlanis arenosa*, for example, were found almost exclusively within 50 cm. of the lake. On the other hand, *Lecane inquieta* was confined to the middle and outer regions of the beaches. In the majority of collections more than 90% of the rotifers occurred in the top 2 cm. of sand.

Apparently the submerged sand near the water's edge is decidedly a less favorable environment than the exposed sand. No harpacticoid copepods were found there and only about a quarter as many rotifers and tardigrades were found as in the sand directly at the water's edge.

Perhaps no other environment is capable of supporting such a dense and diversified group of microscopic organisms as the sandy beach. If a typical 10 cc. sand sample be taken from the surface of the sand at a distance of 150 cm. from the water's edge, it will be found to contain from 2 to 3 cc. of water. Within this small volume will be found 4,000,000 bacteria, 10,000 Protozoa, 400 Rotatoria, 40 Copepoda, 20 Tardigrada, and small numbers of other microscopic Metazoa.

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THE GRASSLAND BIOME*

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* Based on a portion of a thesis, submitted to the Faculty of the Graduate School, University of Oklahoma in partial fulfillment of the requirements for the degree of Doctor of Philosophy, 1939.

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THE GRASSLAND BIOME[1]

INTRODUCTION

Climax grassland communities occur on all of the world's major land masses, and possess marked resemblance and consistency in climates, in floral and faunal types, in growth form, in physiognomy, and in mores characteristics of the component biota. In Russia this community is termed the steppe, in Hungary, the puszta, in South Africa, the veld, and in South America, the pampas; the general term grassland is usually applied to these and to the other equivalent stands throughout the world. A detailed discussion of the grasslands of the world is beyond the scope of this study, but the grassland areas of North America are representative of this type of biotic community. It is the purpose of this study to bring together the results of research and reports on the condition, fauna, flora, and interrelationships as they existed in the North American grassland before settlement by the European races. From a detailed study of these relationships, which existed in a natural equilibrium, it is hoped that a better understanding may be had of the best ways in which the region under survey may be utilized.

In designating the species of plants the nomenclature of Gray's *Manual* (7th edition, 1908) has been followed, except in the case of the grasses, where Hitchcock's *Manual of the grasses of the United States* (1935) has been used. The common and scientific names of the mammals are those given by Anthony's *Field Book of North American Mammals* (1928), and those for birds are from the A.O.U. checklist which has been reprinted in the Naturalist's Guide, pp. 743-758. Scientific names for reptiles and amphibians are those used by Brennan (1937), and those for the insects as found in the most recent general monograph for the group.

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History of the Grassland

The causes and origin of the prairie in particular and of the grassland in general have been much discussed since the early explorers and settlers from Europe began to enter the prairies of North America during the westward march of civilization. The literature on this subject is voluminous and has been reviewed by Shimek (1911); the realization of the fact that biotic climaxes are essentially climatic in cause and continuation was perhaps the greatest step toward the "ultimate truth" regarding the presence of the grassland. It is now generally conceded that during the pleistocene epoch the successive advances and retreats of the glaciers had a profound influence on the

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vegetation regions through the changes of continental climate. Thus, with successive changes of the generalized pattern of continental vegetation, the prairies were driven southward and westward with the changes in relative temperature and moisture efficiencies. During these periods of the waxing and waning of the glaciers the deciduous forest extended likewise farther west and south, thus giving the three strata of humid biotic remains in peat bog (Sears, 1932, 1932a, 1935) and molluscan deposits (Hedges, 1935). During the intervals of glacial regression and forest advance to the north and east, the drier climatic types of vegetation and accompanying biota moved proportionately in that general direction. Relicts of these eastern prairies have been reported in Ohio and Michigan by various authors. It was probably during these periods that the bison reached its furthest extension eastward, stragglers remaining in the eastern forests after the main body of the species had left in favor of the present great plains; herpetological stragglers have been discussed by Schmidt (1938).

In general two regions served as areas of retreat for the biota during the glacial advances: the southeast and the southwest. Gleason (1923) gave the Ozarks importance as an area from which there was post-glacial dispersion. The pollen and molluscan remains farther west, together with certain mesic forest relics (such as the elm-maple relics in Caddo County, Oklahoma, canyons; see Little, 1938) in the western areas would indicate a farther advance westward than would be allowed by accepting the Ozark-center as suggested by Gleason.

The grassland of North America, as is pointed out in later sections, is made up of three major types: the eastern tall-grass prairie, the western short-grass plains, and the central mixed-grass area. This study places chief emphasis upon the first community, the latter two communities being considered in more summarized form.

CLIMATE OF THE GRASSLAND

As has been mentioned above, the climate of the grassland region is largely responsible for its continuance as grassland. All of the grassland or steppe regions of the world are characterized by essentially the same general type of continental climate and distribution of rainfall and temperature throughout the year. Thornthwaite (1931, p. 654) has characterized the climate of the "grassland climax" of North America as subhumid and meso- or microthermal with varying distribution of rainfall during the summer months; in terms of his formulae, these climates may be expressed as CB'rb, CC'rc, CB'db, and CC'dc. As may be shown by means of climographs (Fig. 4), the critical feature determining the vegetation type of a locality in this area appears to be the deficiency of rainfall in the serotinal period (the later portion of the hot season) and this is probably one of the most influential factors in preventing the grassland regions from developing to a

more mesic type, e.g., a climatic deciduous forest. The serotinal deficiency in moisture plays an important rôle in limiting the activity of the smaller animals and plants, giving the "bimodal curve" in seasonal activity throughout the year which is very characteristic of climatic grassland. At the boundaries of the climatic areas which delimit the biota, edaphic factors, chiefly the greater or lesser water-holding capacities of the soils (chresard), play a more obvious part.

TALL-GRASS PRAIRIE

Of the three associations making up the grassland formation, the tall-grass prairie receives the most rainfall. As is pointed out in a later section, this community is divided into four subregions on the basis of the distribution of the characteristic dominants and predominants. These biotic regions, or faciations, thus defined have received special attention from the climatic standpoint, and climographs for several stations in each area are presented in Figure 1. The data for these and the other climographs are based upon the average figures published by the Weather Bureau of the United States Department of Agriculture (1930). Figure 1-F is a summary of the preceding figures and presents a generalized pattern for the prairie region as a whole. This generalized pattern was obtained by drawing a line around the extreme points of the climographs for the subregions. The dotted line represents the climate of the central region; the other regions are represented by continuous lines in Figure 1-F only when their patterns exceed those of the central area. The prairie of Illinois (xxxxxxxxx) has considerably more rainfall than do the other prairie types; it is for this reason that the Illinois prairie and that of immediately adjacent areas is not considered as climactic, since the climate is more favorable for the development of forest (with relatively abundant rainfall the year around) than for prairie, the latter existing here only by edaphic causes. The prairie type of climate is characterized by an arid, cold season of about six months of the year, with a hot season (July and August in North America), broken into a wet and a dry portion.

Climatic factors, however, fluctuate widely from year to year, and, as has been evident from long-term weather records, variations occur in general in cycles. These cyclic variations of temperature and rainfall center about a mean, and the intensity of variation may well be expressed in terms of the mean deviation. In Figure 2 there is superimposed upon the climographs a representation of the mean deviation in the form of "diamonds." The differently ruled diamonds are merely for convenience in reading the graph and have no other significance than to distinguish overlapping figures. From these graphs it will be seen that in Oklahoma City (a typical station in the southern region of the prairie) there is a more intense variation from the mean than further north at Yankton, S. D. In both stations, however, there is a greater variation in temperature during the cold months, and in precipitation during the rainy period. Since it is the minimal or maximal

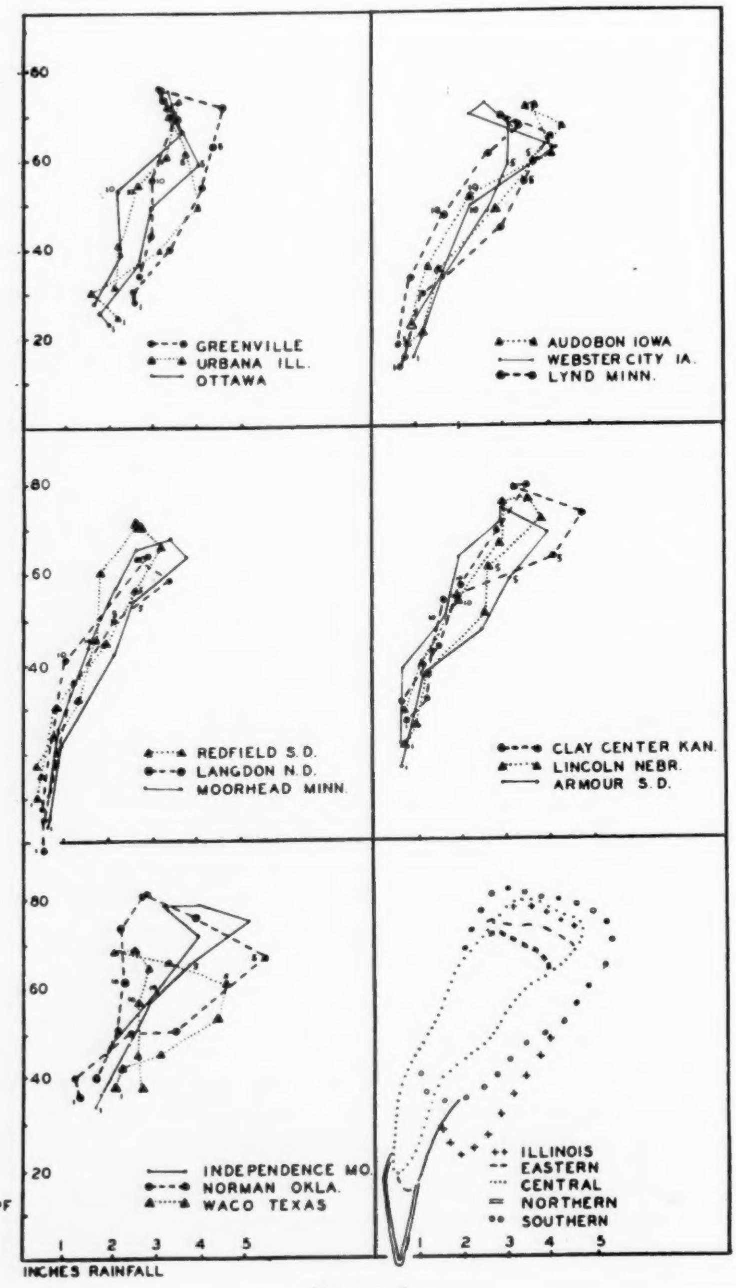
GREENVILLE
URBANA ILL.
OTTAWA
AUDOBON IOWA
WEBSTER CITY IA.
LYND MINN.
REDFIELD S.D.
LANGDON N.D.
MOORHEAD MINN.
CLAY CENTER KAN.
LINCOLN NEBR.
ARMOUR S.D.
INDEPENDENCE MO.
NORMAN OKLA.
WACO TEXAS
ILLINOIS
EASTERN
CENTRAL
NORTHERN
SOUTHERN
°F
INCHES RAINFALL

FIGURE 1

amounts in which any factor occurs which are significant in determining whether or not an organism is able to survive in a given habitat, these periods of variation are of utmost importance. Therefore, the variations from the plotted mean to the left (indicating decreasing rainfall) make for the invasion of plains conditions, and to the right (increasing rainfall), the invasion of forest conditions and species.

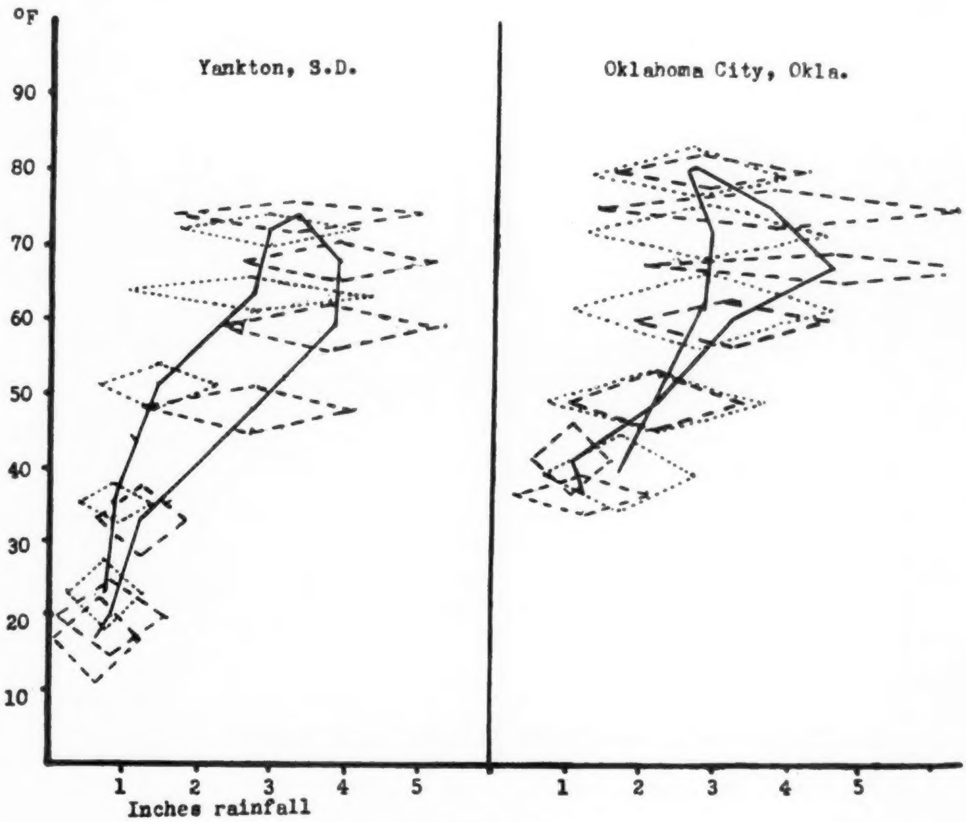

FIGURE 2

MIXED-GRASS AND SHORT-GRASS PLAINS

The climates of the mixed-grass prairie-plains and the short-grass plains have been similarly expressed by climographs (Figure 3). Here the generalized climates typifying the entire areas of both associations are shown in diagrams "D" and "H" respectively. A comparison of the generalized climates for all three associations of the grassland is made in Figure 4; when the patterns of the three climatic types are superimposed, a generalized climographic pattern for the grassland as a whole is obtained.

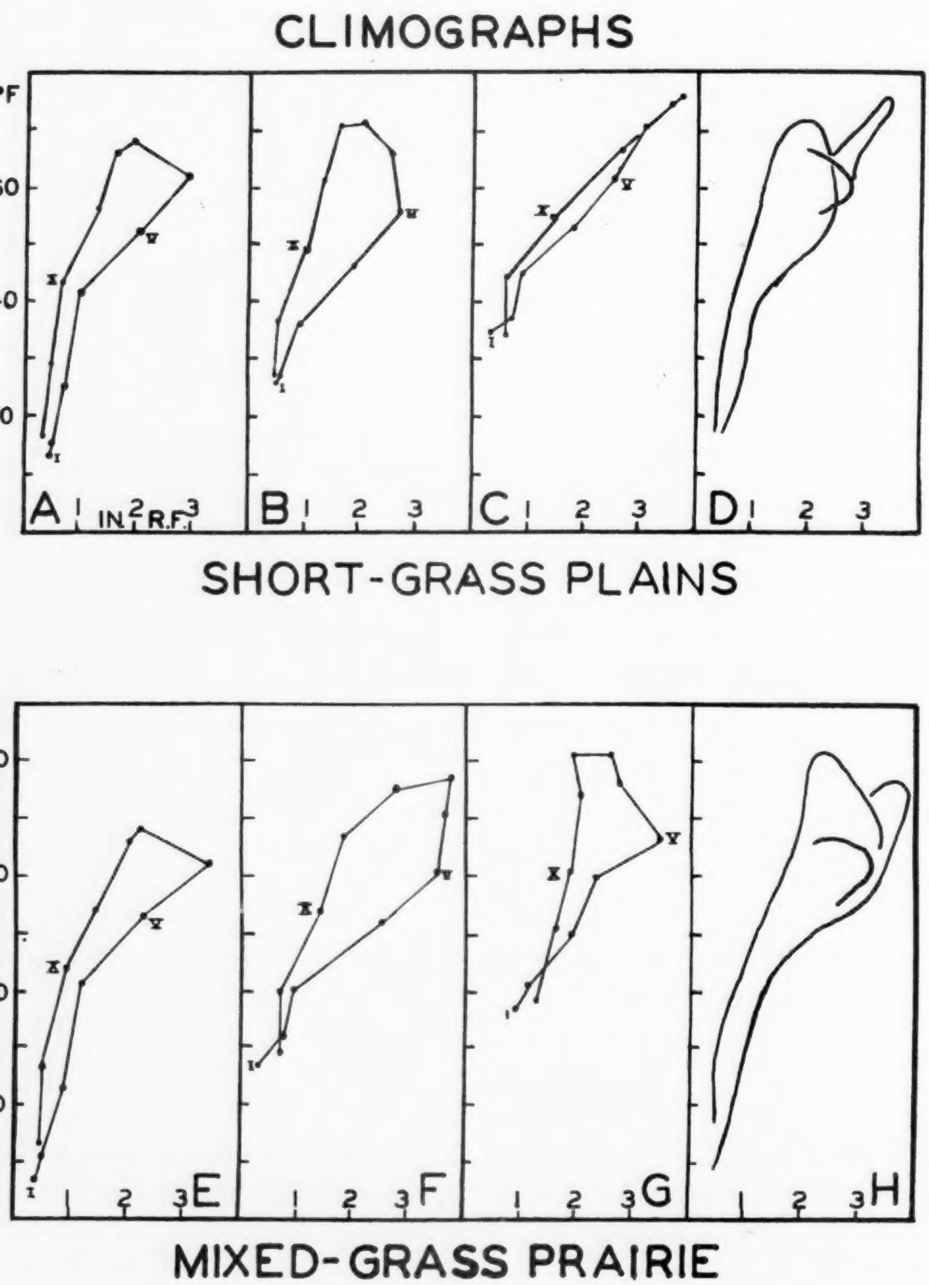
CLIMOGRAPHS
T°F
60
40
20
A 1 IN. 2 R.F. 3
B 1 2 3
C 1 2 3
D 1 2 3
SHORT-GRASS PLAINS
80
60
40
20
1 2 3 E
1 2 3 F
1 2 3 G
1 2 3 H
MIXED-GRASS PRAIRIE

FIGURE 3

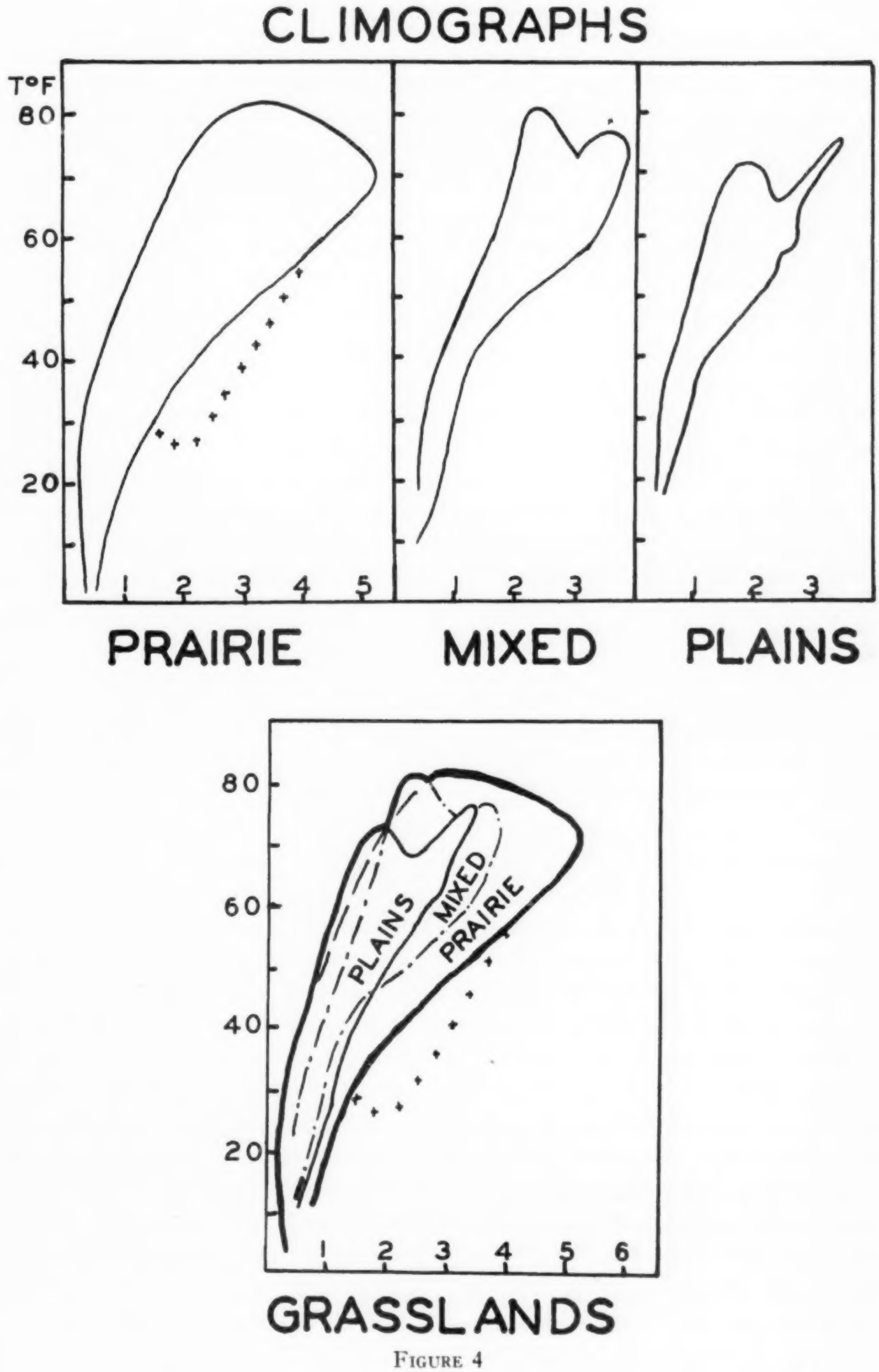
CLIMOGRAPHS
T°F
80
60
40
20
1 2 3 4 5
1 2 3
1 2 3
PRAIRIE
MIXED
PLAINS
80
60
40
20
PLAINS
MIXED
PRAIRIE
1 2 3 4 5 6
GRASSLANDS

FIGURE 4

THE TALL-GRASS PRAIRIE

A biotic community is defined in terms of its biotic components and is recognized by a characteristic structure or organization throughout the area it occupies. The structure of a community is based upon and controlled by those organisms which dominate the community. A community may be delimited, therefore, only by a study of the distribution of the areas where these important organisms exert dominance, not by any physiographic "habitats." The prairie dominants are certain grasses upon which the other life of the prairie community is based. It is the object of this section to bring together the findings of previous studies which have been made on the prairie dominants with the purpose of delimiting the association and its faciations. Mention will be made only of the principal species, the dominants and subdominants when so designated. The lesser subdominants appearing in the several seasonal aspects are considered in a later section.

The papers listed below have been used to obtain descriptive data of the areas which have previously received study. General papers dealing with large areas of the prairie are considered first, and are followed by an outline of the specialized local studies. The latter are taken up by the political regions in which the studies were made purely as a matter of expediency, working from east to west, and from north to south.

The Dominants

A number of important general contributions to the study of the prairie have appeared; one of the first was that of Pound and Clements (1898a, 1900) who published a detailed and now classical study dealing with the regions (prairie, sand hill, and foot hill) of the "prairie province"; while it has particular reference to Nebraska the study considers the prairie (their "region I") as extending southward to central Oklahoma, the "black soil" prairie of Texas being included in their "region II," the sand hills. In 1911 Shimek reviewed the theories on the origin of the prairie, and in 1926 Schaffner published an outline of community composition with relation to physiographic levels within local areas along a transect from central Illinois to western Nebraska. A comparable but somewhat more detailed study by Weaver and Fitzpatrick (1934) dealt with the prairie areas from southern Minnesota and South Dakota to northern Kansas, in general following the Missouri valley. Aikman's (1935) survey of the western border of the tall-grass prairie along the shelterbelt area and Transeau's (1935) review of the general phenomena and causes of the "prairie peninsula" extending into the states of Illinois, Indiana, and Ohio are likewise valuable studies dealing with their respective portions of this biome. Shantz (1938, p. 843), in a general study, divided the "Tall Grass (Prairie Grassland)" into the following:

"Bluejoint sod" (northern and southern parts): "the northern part of the bluejoint-sod grassland lies in the Corn Belt and the southern part in the corn and winter wheat region . . . and . . . the Cotton Belt."

"Porcupine Grass, June Grass, and Slender Wheatgrass . . . occupies the Red River Valley of North Dakota and Minnesota."

"Needle-and-Thread, June Grass, and Slender Wheatgrass . . . from North Dakota south to southern Nebraska."

"Little Bluejoint-Bunchgrass (Bluestem-Bunchgrass) . . . occupies a belt about 100 miles wide running north to south across the middle of Kansas, swinging west to the eastern edge of the Panhandle of Texas and extending across Oklahoma."

The following studies deal with consideration of local areas; those dealing wholly with nonclimatic "sand prairies" are omitted; in this connection the reader should consult the recent work of Ramaley (1939).

Michigan: (small relict prairies) Dice, Jones, and Gaige, Nat. Guide, p. 379; Gleason, 1917; Kenoyer, 1930; Veatch, 1928.
Ohio: Braun, 1921, p. 172, 1928, pp. 288-9, 295, 1928a, pp. 408, 426; Mosely, 1928; Sears, 1926.
Indiana: Deam, 1929, p. 347; Scott, Nat. Guide, p. 372; Welch, 1925.
Wisconsin: Graechner, 1935, p. 293.
Illinois: Adams, 1915a; Hart and Gleason, 1907; Gleason, 1910; Paintin, 1928; Sampson, 1921; Turner, 1934; Vestal, 1913a, 1914a, 1931a.
Minnesota: Ewing, 1924; Rosendahl, Nat. Guide, p. 274; Schaffner, 1926, pp. 10, 12; Stallard, 1929, p. 488.
Iowa: Burk, 1929; Hendrickson, 1930, p. 53; Shimek, 1910, 1911, 1915, 1917, 1924, 1925, 1926; Weaver and Fitzpatrick, 1934.
Missouri: Burrill, Nat. Guide, p. 485; Weaver and Fitzpatrick, 1934, p. 161.
Arkansas: Bucholz, Nat. Guide, p. 466; Harper, 1917.
Manitoba: Bird, 1927, p. 212; 1930, p. 369; Criddle, 1933; Shimek, 1925, pp. 25-36.
North Dakota: Hanson and Whitman, 1938, pp. 99, 106; Switzer, Nat. Guide, p. 545.
South Dakota: Harvey, 1908; Petry, Nat. Guide, p. 549.
Nebraska: Pool, 1913; Pound and Clements, 1900; Steiger, 1930; Thornber, 1901; Weaver and Fitzpatrick, 1934.
Kansas: Schaffner, 1913, 1926, pp. 20, 34, 40-41, 1938; Weaver and Fitzpatrick, 1934, p. 159.
Oklahoma: Blair, 1938, p. 349; Booth, 1932; Bruner, 1931, p. 158; Carpenter, 1939a; Hefley, 1937; Little, 1938; C. Smith, 1939.
Texas: Fletcher, 1930; Tharp, 1926; Whitehouse, 1933.

The "wet prairies" of much of the southern coastal plain should not be confused with the true prairie of the grassland area, since the former, which are essentially marshy areas and sometimes wooded, are not climatically caused (in the usual sense) and are not connected with the grasslands under consideration. For a discussion of the local vernacular including the term prairie in this sense see Wright and Wright (1932, *Ecol. Monographs* 2, p. 119).

DISCUSSION: EAST-WEST VARIATION

Weaver (1919) has pointed out that near Lincoln, Nebraska, on a single hillside the plant distribution is much varied in consequence of edaphic fac-

tors and that "an epitome of decreasing rainfall and consequent mixed prairie and short-grass plains vegetation may be found. . . . The base is clothed with tall grasses and herbs, while the gravelly crest . . . is covered with a nearly pure growth of *Bouteloua gracilis* and *hirsuta*. On the upper slopes the short-grass layer is overtopped by *Koeleria cristata, Stipa spartea,* and *Andropogon scoparius.*"

This same phenomenon has been pointed out and commented upon by Schaffner (1926): by setting up stations across the prairie in a general line from east to west he found that the upland prairie grasses of the eastern prairies move down into the valleys in the middle west and compose the low prairies of the western portions. Data presented by Weaver and Fitzpatrick (1934) for several of their many stations in part substantiate this contention. Thus, in theory, as one moves further westward one finds that the upland prairie species of the east occur in the lower areas. A similar shift of the community in relation to the physiographic habitat has been observed by Bei-Bienko (1930, p. 83) in the study of the ecological distribution of grasshoppers in Siberia and the Zaisian plains. Clements (1934, p. 57) has pointed out that these and similar phenomena have been greatly modified in many cases by human interference.

With the above expressed concept in mind, the data presented in the papers listed as to the dominants and subdominants were analyzed with the purpose of determining the exact relationship of the dominants of the three general edaphic-physiographic areas (high, sloping, and low prairie) to this phenomenon. Accordingly, the degrees of dominance for each species were plotted on distribution maps, and the resultant points of similar expression connected by isophenes. For each species, three of these maps were constructed, one for each of the physiographic levels. Overlay maps for each of these three habitat types are reproduced in Figure 5.

As might be expected, this relationship was borne out by certain species much better than by others. Species which occur as dominants on lower areas in the western portion of their dominance-range, as compared with the habitats in which they are dominants further east, may be listed as *Andropogon furcatus* and *scoparius, Bouteloua curtipendula, gracilis,* and *hirsuta, Bulbilis dactyloides, Panicum virgatum, Poa pratensis* (although a ruderal), *Sorghastrum nutans, Spartina Michauxiana, Sporobolus cryptandrus* and *heterolepis,* and *Stipa spartea.*

NORTH-SOUTH VARIATION

A north-south zonation in the prairie is to be recognized upon an examination of the maps of Figure 5. A climatic explanation of these belts is given by Thornthwaite (1931) who, in delimiting climatic provinces on the basis of efficiency of temperature and precipitation, made the following groupings within the "subhumid" area (see pp. 642, 645, *loc. cit.*):

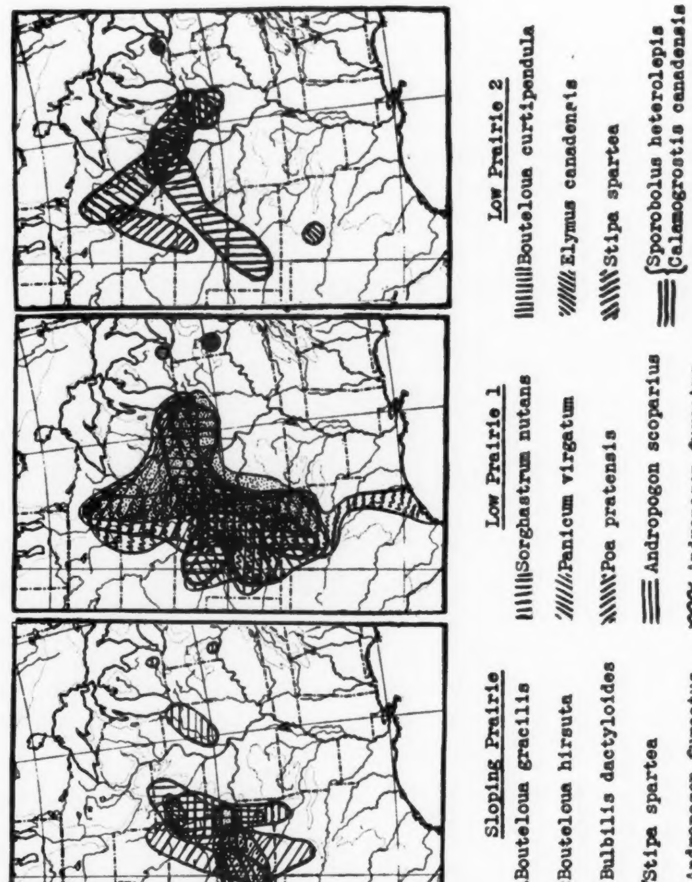
High Prairie 1
Sporobolus heterolepis
Sporobolus cryptandrus
Andropogon furcatus
Andropogon scoparius
Bouteloua curtipendula
Bouteloua gracilis
High Prairie 2
Koeleria cristata
Stipa spartea
Poa pratensis
Bulbilis dactyloides
Panicum virgatum
Bouteloua hirsuta
Sloping Prairie
Bouteloua gracilis
Bouteloua hirsuta
Bulbilis dactyloides
Stipa spartea
Andropogon furcatus
Andropogon scoparius
Low Prairie 1
Sorghastrum nutans
Panicum virgatum
Poa pratensis
Andropogon scoparius
Andropogon furcatus
Spartina Michauxiana
Low Prairie 2
Bouteloua curtipendula
Elymus canadensis
Stipa spartea
Sporobolus heterolepis
Calamogrostis canadensis
Agrostis alba

FIGURE 5

T/E Index	"Province"	States included
128-64	Mesothermal	Texas, Okla., most of Kansas.
48-64	Microthermal	N. Kans., Nebr., S. S.D.
32-48		N. S.D., N.D., W. Minn., Man.

This north-south zonation, to some degree recognizable in terms of the dominant vegetation, is indicated by the distribution of Merriam's "Life Zones" and by Engler's division of this region. Schaffner (1926) comments on this thus: "There is some difference in floral composition between the northern transition prairie region and the southern. In the north *Stipa spartea* and other species are frequent, while they are absent or very rare in the transition prairie of Kansas and southward." Clements (1934, p. 58) contends that this disappearance of *Stipa* and *Koeleria*, at least in the prairies of Kansas, is due to the interference of man and his introduced culture and to semi-domesticated species which have been introduced. It should be recalled that the depredations of the cattle today may to a great degree be comparable to those of the bison which, during their northward migrations under original conditions, also attacked these grasses in their spring anthesis, although their grazing was certainly not as severe nor as consistent as the present-day counterpart. Hildreth (1836, p. 190), in describing the prairie between present-day Oklahoma City and the Wichita Mountains, noted the effects of intensive grazing by bison as follows:

> Upon the prairies the productions that cover different portions are peculiarly distinct; sometimes the tall grass, unmingled with a varied blade, will cover them for miles and miles, like a rich green carpet over a level floor; then again, where immense herds of cattle [bison] are found, the pasturage is cropped close to the earth. On others, the hazel bushes and briars are intertwined, whilst again the broad blossoms of the prickle pear reflects the sun's rays giving the appearance of a molten sea of gold, and affords a lovely and brilliant contrast to the dense mass of green around.

Prairie Types

Regarding the two types of variation in dominance-composition throughout the prairie, several types or faciations are evident in different areas, and at each of the physiographic levels in these regions. A tabulation of the data presented in the literature is given in Table 1 (see Table 4 for a similar tabulation of the seasonal subdominants). From this table it may be seen that as far as dominants are concerned, the prairie has certain species in common throughout and is thus bound together as an essential ecological unit. This may be subdivided into several regional units, which may be caused in part by the geographic affinities of the individual species in question.

AUTECOLOGY OF THE PRAIRIE DOMINANTS

It is upon the ground work of the autecology of individual species that all synecological studies should ultimately be based. Chief attention should be concentrated upon the ecology of the dominants of areas under study. There are many phases of autecological study, each an involved study in itself, but the present discussion is limited to the general ecology and range of the dominant grasses of the prairie areas.

TABLE 1. VEGETATION STRUCTURE OF THE DOMINANTS, TALL-GRASS PRAIRIES

HIGH PRAIRIES
- Binding dominants: *Agropyron repens, Bouteloua gracilis* and *curtipendula*, **Andropogon scoparius.*
- Northern Prairie: *Koeleria cristata, Stipa spartea.*
- Central Prairie: *Panicum virgatum* and *Scribnerianum, Bulbilis dactyloides, Bouteloua hirsuta, Sorghastrum nutans.*
- Central and Illinois Prairie: *Poa pratensis, Sorghastrum nutans.*
- Illinois Prairie: *Sporobolus heterolepis*, **Spartina Michauxiana, Stipa spartea.*
- Southern Prairie: *Stipa leucotricha, Andropogon saccharoides, tener,* and *ternarius.*

SLOPING PRAIRIES
- Binding dominants: none.
- Northern Prairie: *Stipa comata, Elymus canadensis, Agropyron Richardsoni.*
- Central Prairie: *Schedonnardus paniculatus, Sporobolus heterolepis* and *cryptandrus, Bouteloua curtipendula, gracilis,* and *hirsuta, Andropogon scoparius.*
- Central and Illinois Prairie: **Koeleria cristata, Poa pratensis,* **Sorghastrum nutans, Andropogon furcatus, Stipa spartea.*
- Illinois Prairie: **Eleocharis palustris,* **Spartina Michauxiana, Panicum virgatum.*
- Southern Prairie: *Andropogon saccharoides, Panicum oligosanthes.*

LOW PRAIRIES
- Binding dominant: *Andropogon furcatus.*
- Northern Prairie: *Stipa comata* and *spartea, Elymus canadensis.*
- Central Prairie: *Elymus canadensis, Sorghastrum nutans, Koeleria cristata, Panicum Scribnerianum, Bouteloua curtipendula, Andropogon scoparius, Agropyron pseudorepens.*
- Central and Illinois Prairie: **Agrostis alba, Spartina Michauxiana,* **Panicum virgatum,* **Poa pratensis, Sorghastrum nutans.*
- Illinois Prairie: **Calamagrostis canadensis,* **Eleocharis palustris, Sporobolus heterolepis.*

* Species indicated with an asterisk (*) are dominants in the Chicago region, but not elsewhere in Illinois.

Agropyron repens

Areas of dominance:[2] High prairie: c. Okla., n.w. Minn.

Range: "Fields, roadsides, waste places over much of the U. S., mostly in wheat growing country."—Silveus (1933, p. 158). "A naturalized species from Europe and occurs generally as a ruderal."—Deam (1929, p. 101). Newfoundland to Alaska, southw. to Ark.—Hitchcock (1935, p. 231).

(*Agropyron pseudorepens* is found as a subdominant in the low prairie of c. Nebr. *A. Richardsoni (= subsecundum)* is a dominant on mesic areas at Birtle, Man.)

Agrostis alba

Areas of dominance: Low prairie: Chicago and n.e. Iowa.

Range: Across the n. part of the continent and southw. in the mountains. —Hitchcock (1905, p. 25). Cooler parts of U. S.—*Ibid.* (1935, p. 331).

[2] Here, as elsewhere in this section, "area of dominance" refers only to the area within the tall-grass prairie and omits the areas further westward.

(*Agrostis hiemalis* is found abundantly in the low prairie of n.e. Iowa and on middle slopes at Birtle, Man.).

Andropogon furcatus (= provincialis)
Areas of dominance: High prairie: e. Nebr., w. Iowa, s. Minn., c. Ill., oak openings in Ohio.
Sloping prairie: e. & n.e. Okla., n. Kans., Nebr., Iowa, c. Ill., Ann Arbor, Mich., Cincinnati, Ohio.
Low prairie: e. Tex., e. & c. Okla., Kans., e. S. Dak., e. N. Dak., w. Minn.
Range: Que. to Mont., southw. to Fla., Wyo., Utah, and Ariz.—Hitchcock (1935, p. 734).

Andropogon scoparius
Areas of dominance: High prairie: e. Tex., e. & c. Okla., e. Kans., e. Nebr., e. S. Dak., e. N. Dak., Iowa, Chicago, Long Island.
Sloping prairie: n. & e. Kans., s.w. Nebr., w. Iowa, c. Okla.
Low prairie: coastal prairie of Texas, Cincinnati, n. Kans., s.w. Nebr., w. Iowa.
Range: Que. to Alta. and Id., southw. to Fla. and Ariz.—Hitchcock (1935, p. 729).

(*Andropogon virginicus* is found on the high prairie of e.c. Ill. and near Cincinnati in secondary successions on dry hillsides in Ohio; *A. saccharoides* is a dominant in secondary successions from c. Okla. southward, and on high prairie as well as in c. Texas. *A. ternarius* is characteristic of the high prairie of n. Texas and *A. tener* of the coastal prairie of Texas west of the Brazos river.)

(*Aristida* spp. are considered by the majority of authors as species which under original conditions played a part in late hydrosere and psammosere succession. Under the overgrazing practiced by white man (creating a very widespread subsere) they have spread into many new localities and are assuming astonishing proportions.)

Bouteloua curtipendula (= racemosa)
Areas of dominance: High prairie: c. Okla., n. Kans., n.w. Minn.
Sloping prairie: w. Kans.
Low prairie: w. Kans., n.e. Iowa, Cincinnati.
Range: "Most of the U. S."—Silveus (1933, p. 430). Me. and Ont. to Mont., southw. to Ala., Tex., Ariz., and s. Calif.—Hitchcock (1935, p. 513).

Bouteloua gracilis
Areas of dominance: High prairie: w. & n. Kans., n.c. Nebr.
Sloping prairie: c. Okla., c. Nebr., c. N. Dak., n.w. Ill.
Range: Tex. and Mex., northw. to Mo., Colo., Wisc., and N. Dak.—Silveus (1933, p. 428). Wisc. to Alta., southw. to Mo., Tex., and s. Calif.: Mex.—Hitchcock (1935, p. 520).

Bouteloua hirsuta
Areas of dominance: High prairie: S. Dak., c. & n. Kans.
Sloping prairie: c. Okla., c. Kans., c. & e. Nebr., s.e. S. Dak.
Range: Tex. and Mex. northw. to S. Dak., and eastw. along coast to Fla.—Silveus (1933, p. 427). Wisc. to S. Dak. to Tex., Colo., Ariz., s. Calif. and Mex.—Hitchcock (1935, p. 519).

(*Bouteloua texana* = *rigidiseta* is found in subclimax prairies from c. Okla. southward.)

Bulbilis (Buchloë) dactyloides
Areas of dominance: High prairie: w. Kans., w. Okla., n.e. Nebr.
Sloping prairie: w. Kans., w. Okla.
Range: "In varying abundance on the non-sandy soils from the central part of western North Dakota and southeastern Montana to Texas and New Mexico."—Savage (1934, pp. 2-5). W. Minn. to c. Mont., southw. to n.w. Iowa, Tex., w. La., Ariz., and N. M.—Hitchcock (1935, p. 526).

Calamagrostis canadensis
Areas of dominance: Low prairie: c. Ill., Chicago; margin of Lake Erie, drained bogs and wet meadows, Ohio.
Range: Greenland to Alaska, southw. to Md., N. C., Mo., Kans., Colo., Ariz., and Calif.—Hitchcock (1935, p. 315).

Eleocharis palustris
Areas of dominance: Low and sloping prairies: Chicago.
Range: Most of the North American continent; Eurasia.

Elymus canadensis
Areas of dominance: Sloping prairie: n.w. Minn.
Low prairie: s.e. & c. Okla., e.c. Ill., n.e. Iowa, n.w. Minn.
Range: Que. to s. Alaska, southw. to N. C., Mo., Tex., Ariz., and n. Calif.—Hitchcock (1935, p. 257-8).

(*Elymus virginicus* is present as a subdominant in the low prairie of e.c. Ill.)

Koeleria cristata
Areas of dominance: High prairie: e. Nebr., n.w. Minn.
Sloping prairie: Chicago, e. Okla., Birtle, Man.
Low prairie: s.w. Nebr.
Range: Ont. to B. C., southw. to Del., Mo., La., Calif., and Mex.—Hitchcock (1935, p. 277).

Manisuris (Rottboellia) cylindrica
Areas of dominance: High and sloping prairie: e., c., & s.c. Okla.
Range: Coastal plain, S. C. to Fla. and Tex., northw. to Mo. and Okla.—Hitchcock (1935, p. 761). Listed as a dominant of the "Coastal Prairie" by Clements and Shelford (1939, p. 278).

(*Panicum capillare* is considered as subdominant on certain high prairies of the Cincinnati region.)

Panicum Scribnerianum
Areas of dominance: High prairie: n.e. Nebr.
Low prairie: e. Okla.
Range: Me. to B. C., southw. to Md., Tenn., Tex., and Ariz.—Hitchcock (1935, p. 650).

Panicum virgatum
Areas of dominance: High prairie: n.e. Nebr., n.e. Kans.
Sloping prairie: c. Ill., e. Okla.
Low prairie: c. & e. Okla., Kans., c. Nebr., Chicago.
Range: Que. to Me. and Mont., southw. to Fla., Nev. and Ariz.; Mexico and Central America.—Hitchcock (1935, p. 676).

Poa pratensis

Areas of dominance: none:

Weaver and Fitzpatrick (1934, p. 117) stated that this species is found in association with *Andropogon furcatus* 80% of the time in their study of the central prairie. While there has been some difference of opinion as to its origin, this species has been introduced into much of its present range and is a constituent of "pro-climaxes" in many areas, but never assumes dominance in climatically climax prairie.

Range: "Native in the northern U. S., and introduced southward."—Deam (1929, p. 71). "Widely distributed throughout the U. S. and northward, except in arid regions; not common in Gulf states; at all altitudes below alpine regions; introduced from Europe."—Hitchcock (1935, p. 114).

(*Poa palustris* and *nemoralis* are common on the low prairie of n.w. Minn.)

Schedonnardus paniculatus

Areas of dominance: Sloping prairie: c. & n.e. Kans.

Range: Tex. and N. M., Mont., N. Dak. to Ill.—Silveus (1933, p. 391). Ill. to Sask. and Mont., southw. to Tex. and Ariz.; Argentina.—Hitchcock (1935, p. 487).

Sorghastrum nutans

Areas of dominance: High prairie: e. S. Dak., n.e. Kans., w. & c. Iowa, c. Ill., Chicago.

Sloping prairie: Chicago, Cincinnati, n.e. Kans., e. Okla.

Low prairie: c. Ill., n.w. Mo., Ann Arbor, Mich., c. & e. Nebr.

Range: e. U. S. to N. M., Ariz., Tex., and Fla.—Silveus (1933, p. 743). Que. to Man. and N. Dak., southw. to Fla. and Ariz.; Mexico.—Hitchcock (1935, p. 752).

(*Spartina cynosuroides* is found in grassy ravines in n.e. Kansas.)

Spartina Michauxiana (=pectinata)

Areas of dominance: High prairie: Chicago.

Sloping prairie: Chicago.

Low prairie: c. & n.e. Okla., n.w. Minn., c. & e. Ill., n.c. Nebr.

Range: e. U. S. to Colo., and southw. to N. M. and Tex.—Silveus (1935, p. 394). Newfoundland and Que. to e. Wash. and Ore., southw. to N. C., Ill., Ark., Tex., and N. M.—Hitchcock (1935, p. 489).

Sporobolus cryptandrus

Areas of dominance: High prairie: c. Ill.

Sloping prairie: c. Ill.

Low prairie: s.w. S. Dak.

Range: New England to Mont., southw. to Tex. and Mexico.—Silveus (1933, p. 287). Me. and Ont. to Alta. and Wash., southw. to N. C., Ind., La., Ariz., and n. Mexico.—Hitchcock (1935, p. 404).

Sporobolus heterolepis

Areas of dominance: High prairie: c. Ill., Chicago.

Sloping prairie: c. & e. Nebr.

Low prairie: Chicago, c. Ill., Ann Arbor, Mich.

Range: e. Tex. to Mo., Pa. to Conn.—Silveus (1933, p. 284). Que. to Sask. and Wyo., southw. to Conn., Ill., Ark., and e. Tex.—Hitchcock (1935, p. 400).

(*Sporobolus Drummondi* is recorded as a dominant in subclimax prairies of c. Okla.; *S. asperifolius* (= *Muhlenbergia avenacea*) is found in large numbers on slopes in s.e. S. Dak.)

Stipa comata

Areas of dominance: High prairie: w. & c. N. Dak.

Sloping prairie: Alta.

Range: w. Tex. to Minn. and westw. to Calif., Ind.—Silveus (1933, p. 319). Mont. to Wash., southw. to N. M. and Calif.—Hitchcock (1935, p. 430).

(*Stipa leucotricha* is dominant on the high prairie of n.c. Texas, and ranges from Tex. to c. Mexico; *S. patens* is a coastal prairie dominant.)

Stipa spartea

Areas of dominance: High prairie: c. & n.e. Nebr., n.w. Minn., e. & c. Iowa.

Sloping prairie: n.e. Nebr., n.w. Iowa.

Low prairie: n.e. & c. Nebr., n.w. Minn.

Range: Man. to Alta., Mont., S. Dak., and Wyo.—Hitchcock (1935, p. 430).

DISCUSSION

From a study of other features of the autecology of the prairie dominants certain general tendencies may be discerned. The observation of Clements that the forms of immediate boreal origin have an earlier maturation date than do those of southern origin may be noted. Another general tendency is that the distribution of western prairie species in Indiana and Ohio is rather strictly limited to the sand dunes of Lakes Michigan and Erie and of the Kankakee River, showing an inclination towards xerophytism in a climate generally mesic. The habitats selected were the most xeric available in that area. Examples of such distribution include *Agropyron repens* (in part), *Bouteloua curtipendula, Calamagrostis canadensis, Elymus canadensis* (in part), *Koeleria cristata, Panicum oligosanthes, Scribnerianum,* and *virgatum, Sorghastrum nutans, Sporobolus cryptandrus* and *heterolepis,* and *Stipa spartea.* On the other hand, distribution of eastern and Mississippi Valley species in western Kansas is usually along the major river systems, but edaphic limitation is not always so apparent as in the above eastern states. Several good examples are *Agrostis alba, Andropogon scoparius* and *furcatus, Eleocharis palustris, Panicum Scribnerianum, Poa pratensis,* and *Sorghastrum nutans. Stipa spartea* and *Koeleria cristata* are upland species and are limited to the eastern portion of Kansas by climatic, rather than edaphic factors.

The area of dominance is ordinarily less extensive than the general area of distribution for a given species. A rather remarkable exception is that of *Manisuris cylindrica.* This species was found by the writer to be rather important in central and southwestern Oklahoma. Surprisingly enough this is nearly the westernmost record for the species. No explanation can be

made for this phenomenon at the present time, but a more precise knowledge of the habits of this species elsewhere in its range, together with a study of competition met with, might prove enlightening as to the reasons for the species occurring in greatest abundance near the margin of its range.

The Predominants and Influents

In the previous section the ecology of the dominating organisms of the prairie was considered; in the present section are considered in a similar manner the ecology and distribution of the predominating and more influential animals of this community.

The animal life of the prairie has been left to us in a much disturbed state, with but few relics of the predominants. Only such forms as are tolerant of man have persisted and statements concerning the original conditions are to be obtained only from source material written by early explorers and naturalists. Discussions in the current and recent literature frequently give a clue as to the local importance of the animals present both now and originally in the various portions of the grassland and a résumé of these reports is given below.

Faunal Affinities

The faunal affinities of the prairie region have been studied by Adams (1902, 1902a, 1905, 1909) and by Ruthven (1908) and certain aspects of those of the "prairie peninsula" by Schmidt (1938). The discussion of Adams concerning the southeastern United States as a center of dispersal of post-glacial biota has been given above. Ruthven has pointed out that the prairies serve as a meeting place for two faunas (cf. Bessey, 1887), and that the prairies have few forms which are peculiar to them. The conclusions of Ruthven on the effect of the prairie environment on the vertebrate fauna were: (1) the peculiar environmental conditions of the prairie affect the vertebrate fauna either by dwarfing or by the formation of new subspecific characters; (2) most of the forms which inhabit the prairie region either extend into the eastern forest region or into the plains region, or, rarely, into both, few (exceptions being the pocket gopher and the prairie chicken) being confined to the prairie region itself; (3) there is a great difference in the extent to which the forms of eastern North America push westward, or the plains forms push eastward into the prairie region, before becoming checked.

Local Regional Studies

The following outline serves as a guide to the studies which have been published on the predominants and influents of the prairie.

Illinois: *General:* Frison and Miller (Nat. Guide, p. 471), Hart and Gleason (1907), Shelford (1913, pp. 286, 298), Vestal (1913a); *Mammals:* Wood (1910); *Birds:* Forbes (1922), Forbes and Gross (1921, 1923), F. Smith (1930); *Invertebrates:* Adams (1915a), Hebbard (1934, p. 130), Shackleford (1929), Rice (1932).

Wisconsin: *Bees:* Graechner (1935).
Minnesota: *General:* Rosendahl (Nat. Guide, p. 275); *Mammals:* Mohr (1930).
Iowa: *General:* Brumfiel (1918), Pammel (Nat. Guide, p. 481); *Birds:* Guthrie (1928); *Invertebrates:* Hendrickson (1928, 1930, 1931).
Manitoba: *General:* Anderson (1937), Bird (1927, p. 212; 1930, p. 369); *Mammals:* Seton (1909, p. 22); *Invertebrates:* Criddle (1933).
North Dakota: *General:* Bailey (1927), Switzer (Nat. Guide, p. 545); *Birds:* Monsoon (1934).
South Dakota: *General:* Dice (Nat. Guide, pp. 549-551); *Birds:* Over and Thoms (1921, p. 37).
Nebraska: *General:* Wolcott (1918 and Nat. Guide, p. 521).
Kansas: *General:* McColloch (Nat. Guide, p. 515); *Vertebrates:* Dice (1923, p. 50), Linsdale (1927, 1928, 1928a, b, c); *Invertebrates:* Hayes (1927), Knaus (1923), Whelan (1927).
Oklahoma: *General:* Blair and Hubbell (1938), Carpenter (1939a), Hefley (1937); *Mammals:* Blair (1938, pp. 489, 493), Lane (Nat. Guide, p. 495); *Invertebrates:* Acker (1939), Carpenter (1934, 1936a), Davidson and Shackleford (1929), Shackleford (1931, 1935), Shackleford and Brown (1929), C. Smith (1939), V. Smith and Shackleford (1928).
Texas: *General:* Bailey (1903, p. 19), Cahn (Nat. Guide, p. 506); *Invertebrates:* Fletcher (1930), Isley (1937).

AUTECOLOGY AND MORES OF THE PRAIRIE PREDOMINANTS AND INFLUENTS

It has been pointed out by Shelford (*fide* 1932) that the vertebrates have the greatest influence in terrestrial communities. The relative ranking of the larger groups of animals usual for most terrestrial communities is (1) mammals, (2) birds, (3) insects and spiders, and (4) amphibians and reptiles. In considering the several taxonomic groups the above arrangement will be used.

MAMMALS

The primary influences or reactions of herbivorous mammals on their surroundings are frequently much further reaching than the mere devouring of the vegetation which characterizes its habitat. Trampling, if the animal is large, and the cutting of the prairie sod with the hoof are also important items. Attention has recently been called by a number of authors to the presence of certain hormones in the urine of many mammals which stimulate growth in many plants; this is an important interaction which has until recently passed unnoticed or misinterpreted. Many fossorial forms leave heaps of excavated subsoil about the entrances to their dens; these serve as sources of new soil and frequently are the cause of microseres in the immediate vicinity.

The secondary influences of predatory forms are felt only indirectly by the habitat since these forms are further removed, in terms of the food-chain, from the ultimate source of the food supply, the plants. The effects of their predation are exerted on the inanimate habitat only in terms of the entire reaction of the community on its surroundings. In considering any of the

many coactions between animals it is necessary to keep in mind the effect on the community as a whole as well as on the immediate individuals concerned and involved. In this connection a food-chain diagram of the interrelationships of grassland communities in general has been prepared and is included as Figure 6 (p. 660).

Distribution of the Areas of Predominance

The distribution of the areas where the various species of mammals were important has been determined from the reports cited in the outline above. While these reports are much less definite than those for the dominant grasses, certain forms were found to be listed consistently as characteristic influents throughout most of the tall-grass prairie as a whole. Others are characteristic of most of the area, but are absent in some districts; still others characterize more restricted areas. The names of these species have been incorporated into the appropriate portions of the outline of the structure of this community presented below in the final section and are not repeated here.

The Mores of Prairie Mammals

Mores of communities are made up of the habits and physiological characteristics of their component animals and are in many ways comparable to the morphological and physiological adaptations of plants. Mores constitute the ecological adaptations of animals to their surroundings and are, as Shelford repeatedly pointed out in his earlier papers, physiological, rather than morphological. Visher (1916 and Nat. Guide, p. 552) has outlined a number of these adaptations of the fauna of the plains and prairie (with special reference to the mammals, birds, and insects) to which the reader is referred in this connection. An outline survey of the more striking of the mores which may be used to characterize the mammals of the entire grassland is presented as Table 2.

Birds

The population of birds of the prairie, which is composed of comparatively few species, is subject to a marked seasonal fluctuation in numbers, caused, in part, by the autumnal southward and vernal northward migrations of many species. Some species, however, may either remain in position in the central and northern prairies or shift their specific range somewhat to the south during the winter and thus keep the central portion of the prairie populated by some individuals during the entire year. Among the birds of the northern prairie which remain in the general region (and perhaps migrate locally to more protected areas) are the quail, ruffed grouse, prairie chicken, and the sharp-tailed grouse; these may make slight southward shifts in their position in South Dakota according to Over and Thoms (1921). Nearly all of the remainder migrate well to the south and perhaps out of the grassland. Nice (1931, p. 28) listed 16 of the 22 birds considered in this study as

characteristic winter residents of the prairie in central Oklahoma while in South Dakota but two species are noted as being abundant in the winter.

In many instances the bulk of the bird population is resident in the various portions of the prairie region at the same time that the insect population is most active. This of course does not hold for those birds which are "permanent residents" nor for those which leave the northern areas very late in the fall and return early in the spring. However, there appears to be a compensatory (and probably forced) change in feeding habit which enables the

TABLE 2. A TABULATION OF CERTAIN MORES OF GRASSLAND MAMMALS

	Social Life		Stratum			Food Habits			Seasonal Activity		Production of Young		Daily Period of Activity			
	Solitary or Family groups	Herds or Packs	Fossorial, Locally curs.	Fossorial	Cursorial	Herbivorous	Omnivorous	Carnivorous	Migratory	Hibernating	2 litters @ year	1 litter @ year	Diurnal	All 24 Hours	Crepuscular	Nocturnal
Bison		x			x	x			x			x	x			
Pronghorn Antelope	x				x	x						x	x			
Wapiti		x			x	x						x		x		
White-tailed Deer	x				x	x						x			x	x
Mule Deer	x				x	x			x			x			x	
Cottontail Rabbit	x				x	x					x			x		
Jack Rabbit	x				x	x						x		x		
Prairie-Dog		x	x			x				x		x	x		x	
White-footed Prairie Mouse	x				x		x				x				x	x
Prairie Meadow Mouse	x				x		x		x		x				x	x
Prairie Jumping Mouse	x		x			x				x		x		x		
Pocket Mouse	x				x		x				x				x	x
Prairie Harvest Mouse	x				x		x				x				x	x
Franklin Ground Squirrel	x		x				x			x		x	x			
13-lined Ground Squirrel	x		x				x			x		x	x			
Pocket Gopher	x			x		x						x			x	x
Richardson Ground Squirrel		x	x				x			x		x	x			
Wolf		x			x			x	x			x		x		
Coyote	x		x				x					x			x	x
Badger	x			x				x				x			x	x
Bobcat (Lynx)	x				x			x				x			x	x
Shrew	x				x			x			x				x	x
Skunks	x		x					x				x			x	x
Weasel	x				x			x				x			x	x
Prairie Red Fox	x		x				x					x		x		
Kit Fox, Swift	x		x					x				x			x	x

birds to feed on the fruits and seeds to a greater extent during the periods when insects are inactive and harder to obtain. In general it may be said that the food of the prairie birds consists of the most available food in the immediate area during any particular season. During the winter of 1929 Bird and Bird (1931) found that the food of quail in Oklahoma varied widely between various portions of the state and showed that the type of food is important only in its general nature, e.g., seeds, and that while preferences may be shown where there is a wide variety of foods available, the birds will eat what is available in proportion to its relative abundance. With

regard to the predaceous birds (such as hawks) it is interesting to note that here, too, the individuals are absent from the community in the north at the time that their chief items of food (small rodents) are inactive.

Information regarding the distribution of areas where various species of birds are most influential is rather fragmentary. The forms which are important throughout most of the prairie, and which, therefore, may be termed "binding predominants," are the quail, meadowlark, prairie horned lark, bobolink, grasshopper and savannah sparrow, red-tailed hawk, dickcissel, prairie chicken, and upland plover. Other species reported in the literature as characteristic, but for fewer areas, include the mourning dove, kingbird, crow, raven, bronzed grackle, goldfinch, indigo bunting, migrant shrike, vesper, field, lark, and Baird's sparrows, red-winged blackbird, killdeer, sparrow, Swainson's, rough-legged, and Cooper hawks, chestnut-collared and McCown's longspurs, Sprague's pipit, and scissor-tailed flycatcher; other characteristic birds are listed in the outline of the structure of the community in the final section.

Invertebrates

The study of invertebrate populations in communities has concentrated on arthropods—chiefly insects and spiders. It has been found repeatedly that the population of insects and spiders is much greater in seral and disturbed areas than in stands of prairie undisturbed as regards burning (Carpenter, 1939a), plowing and erosion (Fletcher, 1930; C. Smith, 1939), and in undisturbed seral development (Shackleford, 1929; Hefley, 1937). Although Rice (1932) found that there was a decrease in the invertebrate population immediately after burning, Carpenter found that the number of individuals was greater during the rest of the same growing season than in similar nonburned areas.

According to Whelan (1927), the majority (97% in eastern Kansas) of the insects hibernating in grassland are to be found in the ground litter and in the crowns of grasses. Adams (1915a, p. 117) noted similar phenomena in Illinois and also observed that certain insects which hibernate are but barely able to withstand the early unfavorable wet periods of the summer if they are not fully aroused from their winter inactivity; while this wet period is favorable for many eastern species, the later dry period of the summer favors the western more xerophilous species.

A survey of the citations of insect and spider predominance shows that the following species are sufficiently widespread in their importance to be considered as of associational importance:

Melanoplus bivittatus, Ageneotettix deorum, Eugnathodes abdominalis, Œcanthus nigricornis sspp., *Campylenchia latipes, Adelphocoris rapidus, Sinea diadema, Melanoplus atlanis (= mexicanus), Argiope trifasciata, Euschistus variolarius, Diabrotica 12-punctata, Syrbula admirabilis, Hippodamia convergens, Epicauta pennsylvanica, Stictocephala lutea, Orphulella speciosa,*

Xerophloea viridis, Gryllus similis, Deltocephalus configuratus, Scolops spurcus, Dissosteira carolina, Tetragnatha laboriosa.

Species having sub-areas within the tall-grass prairie fall into three groups: those distributed about the central prairie of Iowa and Illinois, the northcentral of Iowa and Manitoba, and the southcentral of Iowa and Oklahoma. Hendrickson's (1928, 1930, 1931) findings are here taken as representative of the central prairie since no equivalent study has been made in eastern Nebraska. Further studies are needed before the members of this very important group can be evaluated in detail.

OTHER INVERTEBRATES

Certain other invertebrates have likewise been mentioned as being characteristic of the prairie: Mollusca cited as abundant or characteristically present are *Zonitoides minisculoides, Gastrocopta contracta* and *arinifera, Pupoides marginatus* (all in Illinois), *Succinea* sp. (Manitoba), and *S. grosvenorii* (South Dakota). Earthworms mentioned include *Octolasium lacteum, Diplocardia communis, Helodrilus trapezoides* (all from Illinois), and *Lumbricoides* sp. (Iowa). Myriopods, reported only from Illinois, are *Pokabius bilabiatus, Nadabus iowensis,* and *Cleidogona caesioannulata.*

REPTILES AND AMPHIBIANS

With but few exceptions little mention has been made in ecological papers of the reptiles and amphibians of the prairie. The forms listed in Table 3

TABLE 3. REPTILES AND AMPHIBIANS OF THE TALL- AND MIXED-GRASS PRAIRIES*

Rana pipiens	Leopard frog	Kans., Man.
Bufo cognatus	Western toad	Kans., Okla., S. Dak., Nebr.
B. woodhousii	Woodhouse's toad	Kans., Okla., S. Dak.
B. americanus	American toad	S. Dak.
Pituophis sayi sayi	Bull snake	Kans., Okla., S. Dak., Nebr.
Tantilla gracilis nigriceps	Mitre snake	Kans.
Thamnophis radix radix	Garter snake	Kans.
T. sirtalis parietalis	Garter snake	Man., Iowa, Ill.
Crotalus viridis viridis	Rattlesnake	Kans.
C. confluentus confluentus	Rattlesnake	S. Dak., Nebr.
Sistrurus catenatus	Prairie rattlesnake	Ill.
Coluber constrictor flaviventris†	Blue racer	Kans., S. Dak.
Heterodon nasicus	Hog-nosed snake	Kans., Nebr.
Lampropeltis triangulum gentilis	Banded king snake	Kans.
L. getulus holbrooki	Salt-and-pepper snake	Kans.
Masticophis flagellum flagellum	Coachwhip snake	Kans.
Storeria occipito-maculata	Red-bellied snake	Man.
Liopeltis vernalis	Green snake	Man., Chicago.
Terrapene ornata	Box tortoise	Kans., Okla., Nebr.
Cnemidophorus sexlineatus sexlineatus	Race runner	Kans.
Holbrookia maculata maculata	Earless spotted lizard	Kans., Nebr.
Sceloporus undulatus consobrinus	Prairie spiny lizard	Kans.
Phrynosoma cornutum	Horned lizzard	Kans., S. Dak. (= *P. brevirostra?*), Okla., Texas.
Eumeces septentrionalis	N. blue-tailed skink	Iowa.
E. fasciatus	Blue-tailed skink	Okla., Ill.

* Scientific names used in this table having reference to Kansas are quoted from Brennan's paper (1937).
† = *Masticophis f. flavigularis.*

regard to the predaceous birds (such as hawks) it is interesting to note that here, too, the individuals are absent from the community in the north at the time that their chief items of food (small rodents) are inactive.

Information regarding the distribution of areas where various species of birds are most influential is rather fragmentary. The forms which are important throughout most of the prairie, and which, therefore, may be termed "binding predominants," are the quail, meadowlark, prairie horned lark, bobolink, grasshopper and savannah sparrow, red-tailed hawk, dickcissel, prairie chicken, and upland plover. Other species reported in the literature as characteristic, but for fewer areas, include the mourning dove, kingbird, crow, raven, bronzed grackle, goldfinch, indigo bunting, migrant shrike, vesper, field, lark, and Baird's sparrows, red-winged blackbird, killdeer, sparrow, Swainson's, rough-legged, and Cooper hawks, chestnut-collared and McCown's longspurs, Sprague's pipit, and scissor-tailed flycatcher; other characteristic birds are listed in the outline of the structure of the community in the final section.

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Species having sub-areas within the tall-grass prairie fall into three groups: those distributed about the central prairie of Iowa and Illinois, the northcentral of Iowa and Manitoba, and the southcentral of Iowa and Oklahoma. Hendrickson's (1928, 1930, 1931) findings are here taken as representative of the central prairie since no equivalent study has been made in eastern Nebraska. Further studies are needed before the members of this very important group can be evaluated in detail.

Other Invertebrates

Certain other invertebrates have likewise been mentioned as being characteristic of the prairie: Mollusca cited as abundant or characteristically present are *Zonitoides minisculoides, Gastrocopta contracta* and *arinifera, Pupoides marginatus* (all in Illinois), *Succinea* sp. (Manitoba), and *S. grosvenorii* (South Dakota). Earthworms mentioned include *Octolasium lacteum, Diplocardia communis, Helodrilus trapezoides* (all from Illinois), and *Lumbricoides* sp. (Iowa). Myriopods, reported only from Illinois, are *Pokabius bilabiatus, Nadabus iowensis,* and *Cleidogona caesioannulata.*

Reptiles and Amphibians

With but few exceptions little mention has been made in ecological papers of the reptiles and amphibians of the prairie. The forms listed in Table 3

Table 3. Reptiles and Amphibians of the Tall- and Mixed-Grass Prairies*

Rana pipiens	Leopard frog	Kans., Man.
Bufo cognatus	Western toad	Kans., Okla., S. Dak., Nebr.
B. woodhousii	Woodhouse's toad	Kans., Okla., S. Dak.
B. americanus	American toad	S. Dak.
Pituophis sayi sayi	Bull snake	Kans., Okla., S. Dak., Nebr.
Tantilla gracilis nigriceps	Mitre snake	Kans.
Thamnophis radix radix	Garter snake	Kans.
T. sirtalis parietalis	Garter snake	Man., Iowa, Ill.
Crotalus viridis viridis	Rattlesnake	Kans.
C. confluentus confluentus	Rattlesnake	S. Dak., Nebr.
Sistrurus catenatus	Prairie rattlesnake	Ill.
Coluber constrictor flaviventris†	Blue racer	Kans., S. Dak.
Heterodon nasicus	Hog-nosed snake	Kans., Nebr.
Lampropeltis triangulum gentilis	Banded king snake	Kans.
L. getulus holbrooki	Salt-and-pepper snake	Kans.
Masticophis flagellum flagellum	Coachwhip snake	Kans.
Storeria occipito-maculata	Red-bellied snake	Man.
Liopeltis vernalis	Green snake	Man., Chicago.
Terrapene ornata	Box tortoise	Kans., Okla., Nebr.
Cnemidophorus sexlineatus sexlineatus	Race runner	Kans.
Holbrookia maculata maculata	Earless spotted lizard	Kans., Nebr.
Sceloporus undulatus consobrinus	Prairie spiny lizard	Kans.
Phrynosoma cornutum	Horned lizzard	Kans., S. Dak. (= *P. brevirostra?*), Okla., Texas.
Eumeces septentrionalis	N. blue-tailed skink	Iowa.
E. fasciatus	Blue-tailed skink	Okla., Ill.

* Scientific names used in this table having reference to Kansas are quoted from Brennan's paper (1937).
† = *Masticophis f. flavigularis.*

have, however, been described as characteristic forms in various localities of the tall- and mixed-grass prairies. The activity of these animals is restricted largely to the spring and summer months when they play an important rôle in these communities in which they may be present in large numbers.

The Subdominants in Aspection

The phenomenon of aspection, or seasonal changes within communities, accompanies the variations of environmental conditions which appear successively throughout a year in a given area and is particularly characteristic of the temperate regions. These successive changes in seasonal "environments" enable many more organisms to live in a given habitat with a minimum of competition for similar basic requirements. Like demands by potentially competing organisms are met by the same habitat but at different times or periods throughout the growing season. We find adaptations on the part of the seasonal forms which enable them to make rapid growth and to undergo their period of greatest physiological activity within a comparatively short period. Groups of such species, all physiologically adapted for growth at a particular time of year, and occurring together during this period, are known as seasonal sociations. Each sociation subsides after the period of physiological activity of its component forms and gives way gradually to a succeeding sociation until the end of the growing season.

The members of these sociations are both plants and animals and are, except during the prevernal period, under the controlling influence of the perennial dominants which are, in the grasslands, the grasses after which the area is named. These seasonal sub-communities, like the perennial nucleus, have certain forms which are more important than others in the ecological structure of the community. These latter forms exert a "secondary dominance" over the remaining forms, and are termed subdominants.

The causes of these successive seasonal appearances are but little known, but are probably due to a multiplicity of interacting factors. Aside from actual exclusion from sociations other than those usual for a species as a result of competition, certain other possibly controlling or interacting factors may be responsible: the presence of an innate seasonal periodicity, a restriction by certain temperatures or humidities (or progressive combinations of both), and the relative lengths of day and night during certain critical periods of the life history. Whatever may be the reason or reasons, they must be omitted as beyond the scope of this study. Their expression in the types of seasonal sociations found in the various portions of the prairie is considered below.

Studies on Aspection

But few detailed studies on aspection in the prairie exist. Seasonal studies have been conducted in Illinois (Paintin, 1928), Manitoba (Bird, 1930), Minnesota (Ewing, 1924), South Dakota (Harvey, 1908), Nebraska (Pound

and Clements, 1898a), and in Oklahoma (Hefley, 1927; Bruner, 1931; Carpenter, 1939a). The lists of plants published by Shimek (1925) and Tharp (1926) for Manitoba and Texas respectively are useful in determining the relative importance of some of the plants in those areas as well. A study of seasonal lists of important plants given by the authors cited above showed that many of the species occur in several of the stations, thus demonstrating a unity and similarity of the various manifestations of each sociation throughout the prairie. These species may be said to bind the prairie together in much the same way as do certain of the dominants. Table 4 was prepared as a summary of these seasonal lists and includes those species which have been recorded as occuring in two or more of the stations. From this table it is evident that certain species are present as binding forms, extending throughout the entire area of the prairie, and that some are restricted to certain of its faciations. It is striking that many of the species spread out from the central prairie area (Nebraska and South Dakota) as a center of dominance-distribution, much as do the dominants, and it is perhaps worthy of comment that this central area of dominance-distribution was the first of the prairie areas to be studied as a community, and has long been taken as representative of the prairie as a whole (e.g., by Clements, Schimper, Harshberger, Warming and Graebner, etc.).

Studies dealing with the aspection of animals have been listed with those dealing with the predominants.

THE EFFECT OF LATITUDE

The difference in the time of seasonal appearance of the species forming the sociations varies both with latitude and longitude. The observations of Hopkins (1918, 1938) which led to the formation of the "bioclimatic law" showed that the average variation between two localities in temperate North America regarding the time of seasonal occurrence of any period event is about four days for each degree of latitude, five degrees of longitude, or 400 feet of altitude, being later northward, eastward, and upward in the spring and early summer, and earlier in later summer and autumn. Gould (1928, 1929, a), working with the appearance of spring flowers in the prairie area, found that for two years the average increase in the rate of appearance of flowers per degree of latitude was five days, and that the eastern stations were later than the western. Weaver and Fitzpatrick (1934, p. 260) note that the difference in the dates of appearance of flowering forms between northern Kansas and southern Minnesota in this regard is from 17 to 27 days (an average of 22 days, or 4.2 days per degree of latitude). In certain cases this change of time of appearance places the organisms in a different seasonal sociation; plants coming under this category are indicated in Table 4 by "*" instead of the usual "+."

TABLE 4. THE SEASONAL SUBDOMINANTS IN ASPECTION

	Man.	Minn.	S. D.	Nebr.	Okla.	Tex.	Ill.
Prevernal Sociation:							
Antennaria campestris	*		+	+	+		+
Anemone caroliniana				+	+		
Draba caroliniana				+	+		
Capsella Bursa-pastoris				+	+		
Androsace occidentalis				+	+		
Vernal Sociation:							
Anemone cylindrica	+	+					+
Lithospermum canescens	+	+					+
Rudbeckia hirta	+				+		*
Geum triflorum	+						*
Lithospermum angustifolium	+		+	+	*		
Phlox pilosa		+					*
Castilleja sessiflora			+	+	+		
Œnothera serrulata			+	+	+		
Anemone caroliniana				+	+		
Baptisia bracteata				+	+		*
Penstemon cobaea					+	+	
Indigofera leptosepala					+	+	
Verbena bipinnatifida					+	+	
Lepidium apetalum					+	+	
Chenopodium album					+	+	
Estival-Serotinal Sociations:							
Penstemon candidum	+	+					
Rosa pratincola	+	+					
Erigeron ramosus	+		+		+		+
Petalostemon purpureum	+	+			+		+
Lilium philadelphicum	+	+					+
Acerates viridiflora	+				+	+	
Rudbeckia hirta	+	+		+	+		*
Amorpha canescens	+	+	+	+	+		*
Verbena stricta			+	+	+		
Plantago Purshii			+		+		
Psoralea tenuiflora					+		
Asclepias verticillata					+	+	
Asclepiodora viridis					+	+	
Psoralea cuspidata					+	+	
Lepachys columnaris				+	+	+	
Œnothera serrulata				+	+	+	
Houstonia angustifolia					+	+	
Krameria secundiflora					+	+	
Silphium lanceolatum					+	+	
Oxybaphus linearis					+	+	
Silene antirrhina					+	+	
Apocynum cannabinum					+	+	+
Autumnal Sociation:							
Liatris scariosa	+	+					
Solidago canadensis	+	+					
S. missouriensis	+	+	+	+			
S. nemoralis	+		+		*		+
S. rigida	+	+	+	+	*		+
Aster sericeus			+	+			
Liatris punctata	+	+			+		
Aster multiflorus	+		+	+	+		+
Helianthus scaberrimus	+	+	+		+		+

Explanation of marks used in table: Species characteristic of an area, but found to occur in anthesis in a different seasonal period than elsewhere are indicated by "*" rather than the usual "+."

THE MIXED-GRASS PRAIRIE-PLAINS

The mixed-grass prairie-plains community receives its name, physiognomy, biotic composition, and much of its ecological structure from its two adjacent associations: the tall-grass prairies on the east, and the short-grass plains on the west. It is, in a sense, a broad area of ecotone, inasmuch as it has features common to those of its two neighbors, and hence constitutes a major area of overlapping. However, this mixed-grass area, in that it is an "area of overlap," possesses certain characteristics peculiar to itself: it is an emergent, and as such attains a certain degree of individuality and is sufficiently stable to be considered as of associational rank.

THE ASSOCIATION

The mixed-grass area as such has, until recently, received much less intensive study than has the tall-grass prairie. The boundaries of the mixed-grass prairie, as here considered, agree essentially with the criteria set by Aikman (cited below); accordingly, both short-grass and mixed-grass communities are treated as individual climaxes, a distinction not recognized by Weaver and Clements (1929, p. 464-5, 1938, p. 524) or Clements and Shelford (1939, p. 260). The community is designated thus:

Andropogon-Bouteloua-Bison-Antilocapra (MIXED-GRASS) ASSOCIATION

"Mixed grass prairie." Vestal, 1914b.
"Xerophytic prairie grass Formation." Vestal, 1914b.
"The mixed prairie: *Stipa-Bouteloua* Association." Clements, 1920, p. 135.
"*Bouteloua-Stipa* (mixed)." Sarvis, 1920.
"Mixed *Andropogon* Association." Schaffner, 1926, p. 9.
"The transition prairie region; Mixed *Andropogon furcatus-A. scoparius* Association." Schaffner, 1926, pp. 27, 50.
"*Agropyron-Festuca-Stipa-Bouteloua* Associes." King, 1927.
"*Stipa-Bouteloua* (mixed prairie) Association." Clements, 1929.
"*Agropyrum-Microtus* Associes of the *Stipa-Bouteloua-Antilocapra-Bison* Formation." Bird, 1929.
"*Andropogon scoparius-Bouteloua curtipendula* Association." Hendrickson, 1930, p. 53.
"*Bouteloua hirsuta-B. curtipendula* Association." Hendrickson, 1930, p. 55.
"Mixed prairie (*Stipa-Bouteloua* Association)." Bruner, 1931, p. 175.
"Climax *Stipa-Bouteloua* Community." Frolick and Keim, 1933.
"*Bouteloua-Bulbilis* Associes." Beed, 1936, p. 21.
"Mixed prairie." Shelford and Hanson, 1936, p. 150.
"Mixed prairie." Albertson, 1937, p. 543.
"Mixed prairie." Brennan, 1937, p. 432.
"The mixed-grass plains [biotic] district." Blair and Hubbell, 1938, pp. 445, 450.
"*Andropogon scoparius-Panicum oligosanthes* (mixed grass) prairie community." Carpenter, 1939a.
"Grama-beard grass Association." Blair, 1938, p. 489.
"Mixed Prairie." Clements and Shelford, 1939, p. 260.

"The mixed prairie: *Stipa-Bouteloua* Association" of Clements (1920, p. 135) extends "from central North and South Dakota, central Nebraska, and northwestern Kansas, throughout Montana and Wyoming to the Rocky Mountains, and southward in Colorado along the foothills of the front range." The "mixed prairie" of Weaver and Clements (1929, p. 464) is more extensive: "from northern Alberta and Saskatchewan through the Staked Plains of Texas and from central North Dakota and Oklahoma on the east to western Wyoming and eastern Utah and southwestward through northern New Mexico and Arizona to the Colorado valley." This great size is due to some degree to the fact that the short-grass areas are included, being considered as a subclimax associes within the mixed-grass association by these authors. A similar view is expressed by Clements and Shelford (1939, p. 260).

The mixed-grass prairie-plains, as here considered, are more restricted in longitudinal width, being considered the area of overlapping of the biota of the short-grass plains and of the tall-grass prairies, i.e., a strip running from central Saskatchewan, northwestern and southcentral North Dakota through central South Dakota, Nebraska (exclusive of the sand hill district), Kansas, and the western part of Oklahoma (exclusive of the Panhandle) to northern Texas. Aikman gives the following description of the boundaries of the area:

> The western boundary of the mixed prairie may be described as a line east of which sufficient rain falls and penetrates the soil to wet it periodically to a depth varying from 24 to 30 inches. Plants whose roots penetrate the soil to a depth of 24 inches or more obtain moisture for sustained growth for a period of at least 2½ months each year, even in drought years. The presence of a permanent tall-grass population is thus insured. The space between these bunches of prairie grasses is occupied by short grasses. On typical upland soil west of the area thus defined, a periodic shortage of water even at a depth of 18 inches precludes the maintenance of a definite permanent tall-grass population within the short-grass cover.
>
> The eastern boundary of the mixed prairie is a line west of which prairie grasses, which assume a bunch-grass habit because of a shortage of available soil moisture, no longer entirely dominate the area but share dominance with short grasses which become permanently established.—Aikman (1935, p. 158).

Schaffner (1926, p. 13) gave as characteristic animals of the mixed prairie in Kansas the prairie-dog and the agricultural ant *(Pogonomyrmex occidentalis)*, and used the eastern boundary of the range of these forms as one criterion for delimiting the eastern boundary of the mixed prairie in this region.

The eastern boundary, except in the north, corresponds closely to the P/E index (precipitation efficiency index) of 48 (see Thornthwaite, 1931). Climographs for the region are presented in Figure 3.

Both from the criteria set by the biota and from those of climate, these boundaries are subject to fluctuation, depending on fluctuation of climatic factors. During dry periods the western more xeric "short-grass" species increase at the expense of the more eastern "tall-grass" species composing the mixture characteristic of the mixed-grass area. Thus in the central Oklahoma study of Carpenter (1939a), the species of grasses which were found to be most abundant in 1934 were found to be on an equal footing with more mesic species in 1938. While this east-west shift in boundary is most noticeable, a similar vertical change on slopes of hills is likewise evident when the conditions during drought and those after several years of normal rainfall are compared. At both of the boundaries there is a wide zone of transition characterized by physiographic vertical zonation, interdigitation, and the presence of "islands" of one community within another.

STUDIES ON THE BIOTIC COMPONENTS

There have been but few studies on the mixed-grass prairie as such. As has been mentioned, many of the essential features and characteristic forms of the mixed-grass prairies are the result of the overlapping of the two neighboring associations. Since this is the case, it has been found most convenient to cite here only those papers dealing with the mixed prairie as such, and refer the reader to the sections dealing with the neighboring communities for a summary of their characteristics.

"The mixed-grass plains [biotic] district is essentially a transition zone between the short-grass plains and the mesophile biota of the tall-grass prairies and eastern forests. Its orthopteran fauna is made up chiefly of short-grass plains species occupying the more xeric habitat types, and the eastern species in the moister situations." Blair and Hubbell (1938, p. 445), who have thus described this area from a zoogeographic standpoint, included lists of those species which were exclusive to their "districts," but those species which are "common to most or all of the districts are omitted, even though they may be abundant and form an important element in the fauna of a certain district." The lists have therefore not been cited here.

The interdigitation or "dovetailing of the prairie and plains" has also been referred to by Schaffner (1926, p. 31): "Just as the flood plain forest extends as long narrow ribbons westward up the ravines and creeks thru the true prairie and the transition prairie, so the *Andropogon furcatus* prairie extends in narrow ribbons up the bottoms of ravines far into the short-grass formation. The transition prairie region, therefore, consists of the mixed *Andropogon furcatus-A. scoparius* association occupying the ordinary levels and areas of ordinary moisture with ribbons and patches of *Andropogon furcatus* on the lowlands, and with *Andropogon scoparius* above the mixed Andropogon prairies, while the highest and driest levels are occupied by the buffalo-grass and the mesquite grasses."

The plant constituents of the community have been studied in Nebraska in the Niobrara Game Preserve by Beed (1936) and in Elkhorn Valley by Frollick and Keim (1933), in western North Dakota by Hanson (1934), in west central Kansas by Schaffner (1926, pp. 27 ff.) and Albertson (1937), and in central Oklahoma by Acker (1939), Carpenter (1939a), and C. Smith (1939), in northern Oklahoma by Blair (1938), and in Oklahoma in general by Bruner (1931). The animals of the following localities have also been studied: Niobrara Game Preserve, Nebraska: Vertebrates and a seasonal study of the invertebrates (Beed, 1936); Ellis Co., Kansas; reptiles and amphibians (Brennan, 1937); Iowa: insects of various prairie communities (Hendrickson, 1930); Oklahoma: Faunal affinities of mammals and Orthoptera (Blair and Hubbell, 1938, p. 450), seasonal studies on invertebrates near Chickasha (V. Smith and Shackleford, 1928, Davidson and Shackleford, 1929, Shackleford and Brown 1929, Shackleford, 1931, 1935), in McClain Co. (Carpenter, 1939a), and in subseres from abandoned, eroded, and overgrazed farmland and prairie (C. Smith, 1939, Acker, 1939) and on mammal populations influenced by overgrazing (Phillips, 1936) and in normal conditions (Blair, 1938).

The ecologically important vertebrates of the community are listed in the outline of the community presented below; the amphibians and reptiles have been included in Table 3 as well.

It becomes apparent from a review of the papers cited above that the dominant grasses of the mixed-grass prairie are those of both the tall-grass prairie and the short-grass plains. The most important dominants throughout are *Bouteloua gracilis* and *hirsuta, Andropogon scoparius,* and *Bulbilis dactyloides,* the latter being absent in the far-northern areas. Little can be said regarding regional faciations until further investigation has been made, but it may be provisionally assumed that the regional variations of the adjoining communities are to be found here as well. The mammals are, in general, more uniform in their distribution than are the grasses, but again the distribution is found to agree closely with that in the adjoining associations. *Citellus 13-lineatus texensis* and *Sylvilagus audobonii baileyi* are species confined to the mixed grass in their range.

THE SHORT-GRASS PLAINS

The short-grass plains constitute the most xeric of the climax associations of the grassland biome. On the east this community is bounded by the mixed-grass prairies, the boundary of which is described in the section dealing with that community. On the west, the short-grass plains meet the series of vegetation zones, alternes, and local complexes of the foothills of the Rocky Mountains. It is problematical whether or not certain of the communities of the mountain front and slopes belong to the grassland biome in the sense in which this term is used in this study. However, some, at

least, of the grassy communities such as "The Short-Grass Association" of Vestal (1914b, p. 385) are affiliated outliers of the short-grass association as considered here; for a detailed account of these communities see Vestal (*op. cit.*, and 1917, p. 373), Shantz (1906), and Hanson and Ball (1928, p. 467).

To the south, in west Texas, the "Mesquite-desert grass savanna" of Shantz (1938, p. 848) is an area of ecotone to the desert types of the Rio Grande region. Its partial grassland character is revealed by the animals characteristic of the area as listed by Cahn (Naturalist's Guide, p. 507): gray wolf, kitfox, coyote, prairie-dog, black-tailed jackrabbit, and Richardson kangaroo rat. Because of its ecotonal character this partially related community will not be taken up here; accounts concerning it may be found in the two works cited and in those of Bray (1901, 1906), Shantz and Zon (1924, pp. 19-20), and Cottle (1931); this area includes types 19 and 78 of Aldous and Shantz (1924) (see Table 5).

[The "bunch-grass (Pacific grassland)" (of Shantz, 1938, p. 849; = "Pacific prairie" of Weaver and Clements, 1939, p. 467; = "California prairie" of Clements and Shelford, 1939, p. 285), the "Palouse prairie" (of Weaver and Clements, 1929, p. 468, and Clements and Shelford, 1939, p. 290), and the "coastal prairie" (of Clements and Shelford, 1939, p. 277) may possibly belong to the grassland biome. Opinion on this matter is reserved, pending more detailed study of their animal components; cf. Clements and Shelford, *op. cit.* The "desert plains," sometimes considered as a grassland, is here taken to belong to the desert complex.]

The short-grass plains community may be designated as the *Bouteloua-Bulbilis-Bison-Antilocapra* (SHORT-GRASS PLAINS) ASSOCIATION.

"Buffalo-Grass Formation." Pound and Clements, 1900, p. 350.
"*Bouteloua* (grama grass) Formation." Shantz, 1906, p. 26.
"Grasslands of the High Plains." Bray, 1906, p. 91.
"Grama-Buffalo Grass Association." Shantz, 1911, p. 24.
"Grama-grass Association." Shantz, 1911, p. 21.
"Grama-grass Formation." Harshberger, 1911, p. 537.
"Buffalo-grass Formation." Harshberger, 1911, p. 528.
"The short-grass Association." Vestal, 1914b, p. 385.
"*Bulbilis-Bouteloua-Poion.*" Clements, 1916, p. 180.
"*Bulbilis-Bouteloua* Association." Clements, 1920, pp. 114, 139.
"Grama grass and Buffalo grass Association." Shantz, 1923, p. 93.
"Grama-buffalo grass." Shantz and Zon, 1924, p. 18.
"Grama-buffalo grass [type 13]." Aldous and Shantz, 1924, p. 102.
"Plains or short-grass Formation." Schaffner, 1926, p. 50.
"*Bulbilis-Bouteloua* Association." Schaffner, 1926, p. 50.
"The Short-grass Subclimax." Weaver and Clements, 1929, p. 468.
"*Bulbilis-Bouteloua* Association." Bruner, 1931, p. 180.
"The Short-Grass Plains." Aikman, 1935, p. 158.
"Grama-buffalo grass." Shantz, 1938, p. 846.
"The short-grass plains [biotic] district." Blair and Hubbell, 1938, p. 450.

"The short-grass Disclimax." Weaver and Clements, 1938, p. 524.
"The short-grass Disclimax." Clements and Shelford, 1939, p. 263.

The most important dominant of the entire short-grass plains community is *Bouteloua gracilis*, the blue grama grass. From South Dakota southward *Bulbilis (Buchloë) dactyloides*, the buffalo grass, is another important dominant. The top few inches of soil are, in good stands of this community, completely occupied by the fibrous roots of the grama and buffalo grasses. The comparative aridity of the area which is occupied by this community may be seen by reference to the climographs presented in Figure 3. A study of the seasonal composition in stands of this community found on the "mesa" near Colorado Springs, Colo., has been published by Shantz (1906, pp. 26 ff.); other seasonal "societies" and "clans" have been listed by Clements (1920, pp. 143-4).

THE FACIATIONS AND PRINCIPAL FACIES

Within the short-grass plains various subdivisions based on plant distribution have been recognized by various authors from time to time. Criteria for the recognition of these divisions have varied with the points of view and purposes of the writers making their studies. Perhaps the most outstanding of these analytical studies have been those of Shantz and his associates (see list of synonomy of this community above for references). In the study of Aldous and Shantz 102 "types of vegetation in the semiarid portion of the United States" were recognized, and index numbers given to each type.[3] These numbers are used for convenience in the accompanying table and in the sections dealing with synonomy in the following discussions to provide a basis of comparison and ready reference, as well as a series of abbreviated designations.

When the short-grass plains are considered as a single biotic association the various natural subdivisions are to be considered as variants of greater or smaller extent within the whole unit: i.e., *faciations*. It is apparent from Table 5 that to a certain extent these types may represent a permutation of possible combinations of the vegetation dominants. However, a study of the geographic areas of extent of the various types shows that certain of them are much more important than are others, and that these wide-spread types subscribe essentially to the more general features of the type of the entire association. The variants of more widely spread occurrence, or faciations, are in turn subject to certain less widely spread (geographically) deletions or additions of local dominants, these forming what are designated in the table as "minor faciations." Other still more local variations or *lociations* may exist which are not here considered.

[3] "The expression 'vegetation type' is here used in the sense employed by foresters to indicate a plant community of any size, rank, or stage of development. It is synonymous with the term 'plant community'."—Aldous and Shantz, 1924, p. 99.

TABLE 5. THE "VEGETATION TYPES" OF ALDOUS AND SHANTZ (1924) ARRANGED ACCORDING TO FACIATIONS

The numbers used are those of the "types" of the above paper. In this table "A" and "B" refer to community types 1 and 2, respectively, as discussed by Hanson and Whitman (1938, pp. 88 and 99).

Association	*Faciations*				*Consocies*
	Major			Minor	
	+		— Buffalo grass	— Buffalo grass + *Carex filifolia*	— Buffalo grass — Grama grass
Buffalo-grama grass		13	1	3	
	W. Needle grass.....	14	12	A	24
	Wire grass	15			22
	W. Wheat grass.....	16	2	B	21
	June grass			4	
	Wild alfalfa	17	9		
	Yucca	18			
	Mesquite	19			
	Matchweed	20	10		25

With but minor exceptions the animal constituency of this association, particularly as regards the predominant mammals, remains essentially the same throughout the entire area. Therefore the divisions or faciations based upon variations in the composition of the plant dominants are taken up first and the faciations defined. This is followed by a section dealing with the animal predominants and influents. It is possible that the faciations may likewise be expressed in terms of differences in the composition of smaller-animal populations, but further study is needed before this can be done.

The following major faciations, together with their respective minor or sub-faciations and facies and consociations (consocies) are recognized within the association:

Bouteloua-Bulbilis-Bison-Antilocapra Association
—*Bulbilis dactyloides* Faciation (Consociation)

"*Bouteloua* type, Buffalo grass Formation." Pound and Clements, 1900, p. 390.

"The *Bouteloua* (grama grass) Formation." Shantz, 1906, p. 26.

"Grama grass Association." Shantz, 1923, p. 92.

"Grama grass." Shantz and Zon, 1924, p. 18.

"Grama grass [type 1]." Aldous and Shantz, 1924, p. 100.

"*Bouteloua gracilis-B. hirsuta* Association." Schaffner, 1926, p. 50.

"Blue grama grass." Shantz, 1938, p. 847.

Distribution: E. Wyo., c. & e. Mont., s.w. Sask., s.e. Alta.

"The dominant plant in this association is grama grass (*Bouteloua gracilis*). With this there are also found in many places *Carex filifolia*, *C. stenophylla*, *Koeleria cristata*, and a wide range of herbaceous plants such as *Artemisia frigida* and *Phlox hoodi* in the north and *Gutierrezia sarothrae* in the south."—Shantz, 1923, p. 92.

Minor Faciations and Facies:

+ *Carex filifolia.* Aldous and Shantz, 1924, "type 3."
+ *Koeleria cristata* and *Selaginella* sp. Shantz, 1938, p. 848.
+ *Muhlenbergia Torreyi.* Shantz, 1938, p. 848.

B-B-B-A Association
+ *Stipa comata* } Facies
— *Bulbilis dactyloides* }

"Grama and western needle grass Association." Shantz, 1923, p. 94.
"Grama-western needle grass." Shantz and Zon, 1924, p. 19.
"Grama and western needle grass [type 12]." Aldous and Shantz, 1924, p. 102.

Distribution: n. & c. S. Dak., c. & w. N. Dak., n.e. Mont., s.w. Sask.

"The appearance of this association is much more varied than that of almost any other portion of the short-grass formation. Except during years of extreme drought the plant cover does not look like a mat of short grasses. The short grasses are important but are overtopped by taller grasses and herbaceous plants. This association is dominated by grama grass *(Bouteloua gracilis)* mixed with western needle grass *(Stipa comata)*. With these dominant grasses there occur other important grasses and many herbs such as *Psoralea argophylla* and *Echinacea* [*Brauneria*] *angustifolia*."—Shantz, 1923, p. 94.

Minor Faciations and Facies:

+ *Bulbilis dactyloides.* Aldous and Shantz, 1924, "type 14."
— *Bouteloua gracilis* [= *Stipa comata* Consocies]. Aldous and Shantz, 1924, "type 24."
+ *Koeleria cristata.* Shantz, 1938, p. 845.
+ *Carex filifolia.* Hanson and Whitman, 1938, p. 89.

B-B-B-A Association
+ *Agropyron Smithii* Faciation

"*Agropyron* Formation." Pound and Clements, 1900, p. 385.
"*Agropyron occidentale* Consocies." Shantz, 1906, p. 36.
"*Agropyron* growth of prairie crests." L. Harvey, 1908, p. 279.
"Wheat-grass Association." Shantz, 1911, pp. 21, 48.
"The wheat-grass Association." Vestal, 1914c, p. 387.
"Western wheat-grass Association." Shantz, 1923, p. 96.
"Western wheat-grass." Shantz and Zon, 1924, p. 19.
"Grama-buffalo, and wheatgrass." Aldous and Shantz, 1924, p. 102.
"Blue grama, buffalo grass, and bluestem." Shantz, 1938, p. 847.

Distribution: c., s., & w. S. Dak.

"This association in its typical form consists of a dense cover of grama grass *(Bouteloua gracilis)* and buffalo grass *(Bulbilis dactyloides)* through which there is evenly scattered a growth of western wheat-grass [= "bluestem" *sensu* Shantz 1938] *(Agropyron smithii)*."—Shantz, 1923, p. 96.

Minor Faciations and Facies:

— *Bulbilis dactyloides.* Aldous and Shantz, 1924, "type 2."
+ *Carex filifolia* (= "Western wheat-grass-grama-sedge type") Hanson and Whitman, 1938, p. 98.
(*Agropyron Smithii* Consociation.) Aldous and Shantz, 1924, "type 21."

B-B-B-A Association
+ *Aristida longiseta* Facies

"Wire grass Association." Shantz, 1923, p. 95.
"Grama and buffalo and wire-grass Association." Shantz, 1923, p. 95.
"Wire grass." Shantz and Zon, 1924, p. 19.
"Wire grass." Shantz, 1938, p. 846.

Distribution: s.w. Nebr., w. Kans., e. Panhandles.

"In appearance the wire grass association is more varied than the typical short-grass cover. The ground is covered by a mat of short-grasses. Overtopping this mat the wire grass and other tall plants may become so dense as to obscure the short grasses entirely. The wire-grass association is an abbreviated name for what in full should be grama and buffalo and wire-grass association. Both grama grass *(Bouteloua gracilis)* and Buffalo grass *(Bulbilis dactyloides)* are grasses of great importance in this area, but with these there occurs a relatively even stand of wire-grass *(Aristida longiseta)*. This association is a more luxuriant phase of the grama and buffalo grass association."—Shantz, 1923, p. 95.

Minor Facies: (*Aristida longiseta* Consocies.) Aldous and Shantz, 1924, "type 22."

PREDOMINANTS AND INFLUENTS

There have been few intensive studies published on the animal components of the short-grass plains. A good characterization of the northern plains, based upon observations in eastern Wyoming and central North Dakota, South Dakota, and Nebraska has been presented by Visher (1916; reprinted in part in Naturalist's Guide, pp. 551-5). Other, but more brief, descriptions of more local areas were also given in the Naturalist's Guide by Elrod for Montana (p. 538), Ramaley and Robbins for Colorado (p. 524), Wolcott for Nebraska (p. 521), Dice for South Dakota (p. 550), and McColloch for Kansas (p. 516). A description by R. M. Anderson (1937) for the entire northern reaches of both prairie and plains in Canada applies here to Manitoba and the mixed-prairie districts of Saskatchewan. Blair and Hubbell (1938, pp. 450-1) have characterized the "short-grass plains [biotic] district" of Oklahoma from the faunistic standpoint with special reference to the mammals and Orthoptera. It is apparent from these citations that many of the predominant animals are uniformly present throughout the entire plains association, illustrating a much greater uniformity than is shown for many of the plant dominants. In this instance, apparently the faciations of the presociations (i.e., of the influent animals) differ in their boundaries somewhat from those of the plants, a difference not found so markedly expressed in the tall-grass prairie. In the outline of the structure of this community (p. 664) the regional variations of the presociations are listed together with similar regional variations of the plant dominants.

EDAPHIC WOODLAND INCLUSIONS OF THE GRASSLAND

While the biotic communities of the grassland are typically any of the three associations described in the previous pages, there exist within this biome many other communities: edaphic, dis-, pre-, and postclimax inclusions, and seral communities of various kinds. Among the latter may be mentioned such "natural" successions as those arising from sandhills (*cf.* Ramaley, 1939) and river floodplains (*cf.* Hefley, 1937), and man-caused subseres resulting from abuse and overuse of the land, resulting in erosion and a slow recovery after eventual abandonment (*cf.* C. Smith, 1939, a). Other communities have developed to a fairly stable subclimax stage which lasts for varying lengths of time; among these are several types of woodland.

All of these seral communities are considered as subclimax to the climaxes of the biome, and as such are parts of the biome and its climaxes, and not merely units leading up to the climax stage. While not, perhaps, continuously represented over a great area, the ranges of these (and other) associes are frequently as great as are those of the associations of which they are components. While superficial examination points to the validity of this concept with reference to a number of the seral communities which have been noticed and described, it perhaps can be illustrated best through the use of the edaphic woodland communities included in the grassland, a series of communities which has received attention in several widely distributed studies.

With the exception of the floodplain forests, the forest and forest-edge inclusions of the grassland are characteristic of the area of ecotone between the eastern deciduous forest and the prairie. This tension zone or ecotone illustrates very well the principle that similar communities are separated by ecotones of zonation and dissimilar communities by alternation, the "similarity" here referring to the growth form of the dominants. It is not surprising, therefore, that gradual zonation from forest to prairie is not usual; in most cases rather abrupt changes from forest to prairie are found, and these may be repeated as "alternes" which are largely dependent on edaphic conditions. In certain cases these alternes may be very wide in themselves and, if wooded, may contain true forest conditions in their interiors which are buffered from the rigors of the grassland climate by a forest-edge of thicket. This latter type of forest-edge has been designated as an "ecotone of the second order" in contrast to the general ecotone area. While this *parkland* aspect is assumed for the most part, there is some *savanna* where trees, mostly isolated, are present and the ground is covered with grasses instead of the ground cover usual for a forest interior. In the following discussion the floodplain forests and the larger forests of the upland are omitted.

THE FOREST-EDGE COMMUNITY

The isolated prairie groves of Illinois have been studied by Vestal (1931b) who classified them into two general types: the "elm" type and the "hackberry" type. In an earlier study (1914a) the same author described the composition of the zones of vegetation found in forest-edges near Elmhurst, Ill. Studies on the aspection and diurnation of the plants and invertebrates in a forest-edge community near Urbana (the "*Cercis-Cornus-Cardinalis-Ceratomegilla* Associes") have been reported by Carpenter (1935), as has a study of the birds of the same community (1935a). Another study of the aspection of the animal components (the "*Helodrilus-Euscelis* Presocies") of a nearby forest-edge stage in a forest sere has been reported by V. G. Smith (1928). The general plant ecology of the adjoining upland forest has been studied by MacDougall and associates (1922, 1925, 1928), and by Telford (1926), and the ecology of the animals by Weese (1924, a), Blake (1926, 1931), V. G. Smith (1928), Townsend (1928), Davidson (1930, 1932), and Beall (1935). A comparison of these studies shows that there is a much greater animal population in the forest-edge than in either of the two adjoining communities, the forest interior or the adjoining prairie (Shackleford, 1929), and that this population undergoes a greater fluctuation both seasonally and daily than do those of the adjacent communities (see Carpenter, 1935, 1936a).

The following studies have been published on the ecology and biotic composition of forest-edges in various other localities: Nebraska: Aikman (1929), Beed (1936, p. 24), Hanson (1922), Pool, Weaver, and Jean (1918, p. 31), Pound and Clements (1900, p. 324); Minnesota: Rosendahl (Nat. Guide, p. 273), Stallard (1929, pp. 489, 514); Iowa: Aikman (1929a); Manitoba: Bird (1927, p. 214; 1930); Kansas: Dice (1923, p. 48); Oklahoma: Blair (1938, pp. 479, 490), Bruner (1931, p. 156), Carpenter (1937), Hefley (1937), Little (1938, p. 24).

The names of the dominants of the woodland communities described in the studies cited above were tabulated in a manner similar to that employed in the case of the prairie grasses, the result corresponding rather closely with the findings of Aikman's important study (1935) on the native vegetation of the Shelterbelt region which included much of the western border of the prairie. The more widely distributed and ecologically important species in this trial tabulation and those of Aikman's table (his figure 78) were incorporated together and are presented here as Table 6. An inspection of this table shows that a number of species are found consistently in similar forest-edge communities throughout the entire prairie area, and that some are more restricted in their ecological range of dominance than are others.

The species in this table constitute throughout the prairie several types of associes which are closely related both in their positions in the local seres and in biotic composition. Considered together, these communities constitute

TABLE 6. BINDING FOREST-EDGE AND SAVANNA SPECIES

Species	Ill.	Man.	Minn.	N. D.	S. D.	Nebr.	Kans.	Okla.-Tex.
Ulmus americana	*			A	A	A	A	A
Celtis occidentalis	*			A	A	A*	A*	X*
Craetagus spp.	*			A	A	X*		*
Prunus americana	*	sp.	*	A	A	A*	A*	X*
Prunus virginiana	*	*	*	A	A	A*	X*	X*
Tilia glabra	*			X	X			
Fraxinus campestris	?			A	A	A,sp.	X	X,sp.
Cercis canadensis	*					*	*	X*
Rubus occidentalis	*		sp.	X	X	X,spp.		
Amorpha canescens				X	X	X	X	X
Amorpha fruticosa	*						*	*
Rhus Toxicodendron	*			X	X	X*	X*	X
Vitis vulpina	*			X	X	X*	X*	X*
Parthenocissus quinquefolia	*			X	X	X*	X	X*
Cornus asperifolia	sp.		sp.			A*	A*	X*
Cephalanthus occidentalis	*						X	X*
Populus tremuloides		*	*	A	X			
Rosa pratincola	sp.	sp.	sp.	X	X	X	X*	X
Rhus glabra	*			X	X	X*	X*	X*
Amalanchier humilis		sp.	spp.	A	A	X,sp.		
Symphoricarpos occidentalis		sp.	sp.*	A	A	X*		
Arctostaphylos uva-ursi		*	*					
Corylus americana		*	*			*		
Evonymus atropurpuratus			*			*	*	
Rhus spp.			*				*	*
Sambucus canadensis			*		X	X*	X*	X*
Viburnum Lentago			spp.	X	X			
Rhus trilobata						X	X	A*
Acer Negundo				A	A	A	A*	X*
Quercus macrocarpa				A	A	X*	X	A*
Ribes aureum, R. odoratum				A	A	A	X	X
Ribes americanum				X	X	X		
Grossularia spp.				X	X	X		
Xanthoxylum americanum				X	X	X*	*	
Celastrus scandens				X	X	X*	X*	X
Shepherdia argentea				A	A	A	A	
Smilax hispida						*	*	*
Symphoricarpos orbiculatus						X*	X*	X*
Baccharis salicina							X	X
Celtis reticulata							A	A
Prunus angustifolius							X	A*
Diospyros virginiana								X*

Explanation of marks used in table: A = species considered as "ecologically important" in Aikman's (1935) report; X = other species listed for more than one area by Aikman; * = species listed as ecologically important in other papers; sp. and spp. = one or several species of the same genus present, but different from that listed in the table.

a "complex of associes," the counterpart of similar "preassocies complexes" of animals which have been described (see Carpenter, 1936, p. 287). This entire complex of forest-edge associes is distributed, with regional facies, from Illinois to western Kansas, and from Manitoba to Oklahoma. It may be named, in terms of its characteristic dominants, the *Prunus-Rhus-Celtis-Vitis* COMPLEX OF FOREST-EDGE ASSOCIES, a designation which reflects the names which have been assigned to its stands throughout the prairie region.

The principal species of plants of this complex include *Prunus americana, P. virginiana, Rhus glabra, R. Toxicodendron, Celtis occidentalis, Cercis canadensis, Vitis vulpina, Ulmus americana* (young individuals), *Cractagus* spp., *Fraxinus campestris, Rubus occidentalis, Psedera (Parthenocissus) quinquefolia, Cephalanthus occidentalis.* Species restricted in their distribution as dominants to the climatic prairies (and hence less characteristic of the forest-edges of Illinois) are *Rosa pratincola, Amorpha canescens, Acer Negundo, Quercus macrocarpa, Ribes aureum, R. odoratum, Celastrus scandens, Sambucus canadensis, Symphoricarpos occidentalis* and *S. orbiculatus.*

The northern, central, and southern regions possess facies of this complex as follows:

Northern:

+ *Tilia glabra, Populus tremuloides, Arctostaphylos uva-ursi, Corylus americana.*
— *Cercis canadensis, Symphoricarpos orbiculatus.*

Central:

+ *Cornus asperifolia, Corylus americana, Evonymus atropurpuratus, Ribes americanum, Grossularia* spp., *Xanthoxylum americanum, Smilax hispidus.*

Southern:

+ *Amorpha fruticosa, Rhus trilobata, Smilax hispidus, Baccharis salicina, Celtis reticulata, Prunus angustifolia, Diospyros virginiana.*
— *Symphoricarpos occidentalis.*

The latter three facies are termed by Aikman (1935, pp. 165-9) the northern, central, and southern divisions of the upland forest types of tree and shrub communities. The application of ecological methods in the planning for the Shelterbelt Project proved very useful in the determination of the species which were most suitable for planting in the area. In effect, the purpose of the Project was to foster the development of the communities which make up the forest-edge and thicket complex.

Local Community and Environmental Complexes

In the above section attention was called to the fact that certain seral stages may be bound together into complexes in that they have important dominant species in common, these complexes considered above in the abstract from the standpoint of their general distribution throughout the prairie area. When concrete examples ("stands") of communities in a given area are examined, phenomena may be observed which give an insight into some of the many interrelations which exist between adjacent communities in a local complex.

Local environmental complexes of communities are most frequently found in areas of ecotone but may be present everywhere that succession occurs or where several communities come into contact with each other. Their presence

is characterized by several or many forms—dominants, subdominants, predominants, or influents—which may range from one community to another or be common to several adjacent communities which are hence bound together, even though they may be distinct in growth form and other ecological characteristics. In some instances several successive stages in a sere may be different physiognomically and have different dominants, but they still may have some of their constituents—both plants and animals—in common. In such instances *complexes of associes* are recognized.

When the binding perfluents (as the organisms common to several adjacent communities have been termed) are plants, they frequently are indicators of invasion or succession, but the perfluent animals may have an additional significance—that of indicating the degree of tension of ecological factors as illustrated by such frequent migrations as occur seasonally and daily.

It is only in cases where many communities in a local area have been carefully studied that these interrelations and migrations can be analyzed or even recognized. This phenomenon of migration was first recorded by Weese in his study of an elm-maple forest in Illinois (1924), when attention was called to the seasonal migration of insects through the forest-edge into the surrounding territory each spring, and a return migration back into the forest in the autumn. Brown (1931) found less evidence of this phenomenon in Missouri and nearly an absence of it in Oklahoma where she worked with stations well within an upland forest. Both Hefley (1937) and Carpenter (1937), working in Oklahoma in areas where the ecological tension was more evident, found migration seasonally and daily between adjoining communities. In the complex of communities of wooded ravines and surrounding prairie in McClain County, Oklahoma, near Norman, seasonal migration was found to be most characteristic of insects spending the winter as adults or late larval instars. In the early spring they are active in the habitat where they spend the winter, and subsequently migrate to their summer feeding and breeding areas. Of the more migratory species studied, about 75% had this type of life cycle. The remainder of the migratory species—those shifting their place of greatest abundance as the year advanced—did not appear as adults until the estival period. Since adults were never taken during the winter period it is presumed that these species spent that part of the year as eggs or early instars.

The species considered were classified by Carpenter (1937) as follows, according to their migration behavior: (1) species which are characteristically prairie forms, spending the winter in that habitat, and moving into more protected areas during the summer or autumn for shelter from less clement environmental factors of the upland, or in search of the more succulent food in wooded ravines; (2) Species which spend the winter in sheltered communities, such as grassy or wooded ravines, and move to the higher

prairie during the summer; (3) species which migrate vertically from the duff to the tree strata in the wooded areas, following the seasonal shift in maximum leaf surface; (4) another type which was observed in several cases involved migration from the principal habitat during the seasons of maximum abundance which seemed to serve as an outlet of "overflow" for the surplus numbers. Usually some individuals of these species were to be found in all habitats during the period of abundance in the principal habitat.

ECOLOGY OF THE GRASSLAND BIOME

THE UNITY OF THE BIOME

The biota of the North American grassland studied is ecologically similar to those of the other steppe regions of the world. The nearctic grasslands constitute a natural area which, while showing many east-west and north-south variations, contains certain essential features which are present throughout the entire range. A common physiognomy, a constant growth form on the part of the dominants, a similar ecological structure throughout, the presence of essentially similar climographic patterns in all sectors, and a homogeneity of the larger predominant forms in most of the areas of the community, are all elements which bind this community together into an ecological unit having the rank of a biome or biotic formation.

Climatically, the prairie plains may be characterized as having a subhumid micro- or mesothermal climate with varying distribution of rainfall during the summer months. As may be shown by means of climographs (see Figs. 1-4), the critical feature determining the vegetation type of a locality in this area appears to be the deficiency in rainfall in the serotinal period, the latter portion of the hot season. This plays an important role in limiting the periods of activity of the smaller animals and plants, giving the "bimodal curve" in seasonal activity throughout the year which is very characteristic of climatic grassland. At the boundaries of the climatic areas which delimit the biota, edaphic factors, chiefly greater or lesser water-holding capacities (chresard), play a more obvious part.

The hemicryptophytic growth form is characteristic of the dominants of the entire biome, although a few minor species assume the rhizome-geophytic growth form; physiognomically the two groups are identical.

The ecological structure of all of the climax communities making up the grassland biome is essentially the same. The ecological structure of a community refers to the organization of the ecological niches within the community and the interrelations of the biota occupying them. Organisms occupying a given niche in a community (or in several communities) are said to be "doing" similar things and occupying identical positions with reference to their associated biota; for example, both ruminants and lagomorphs are comparatively large herbivors, are potent consumers of the vegetation, and

occupy the position of transforming grass food into a condition in which it can be consumed by the predators. Ecologically the two types of herbivors occupy equivalent places in the ecological structure of the community. More than one species may occupy a given niche in a given area, and hence enter into active competition and, in certain instances, a niche may be unoccupied through the non-availability of suitable forms. A given niche may be occupied in one portion of a community by certain forms, and in another by other species or subspecies or possibly by unrelated forms, the ecological structure of the community, however, remaining essentially the same. This phenomenon is particularly to be noted in the behavior of the ecologically equivalent species and subspecies of the genera *Peromyscus, Sylvilagus, Citellus* (*13-lineatus* sspp.), *Canis* (coyote group), and *Perognathus.*

Elton has pointed out that the animals occupying the various niches are usually of different sizes and abundances, and that the greatest numbers of animals are those feeding directly on the vegetation. A smaller number of animals feeds on these phytophagous forms, a third group feeds on the second, and so on. Each of these successive groups is composed, in general, of fewer and frequently larger forms. This phenomenon he has expressed as the "pyramid of numbers" concept, a concept for which examples may be found in practically all communities: a decreasing number of forms in the niches which are further removed from direct dependence upon the plants.

One of the simplest methods of showing a complex set of interrelations within a community is that of depicting the food relationships graphically in

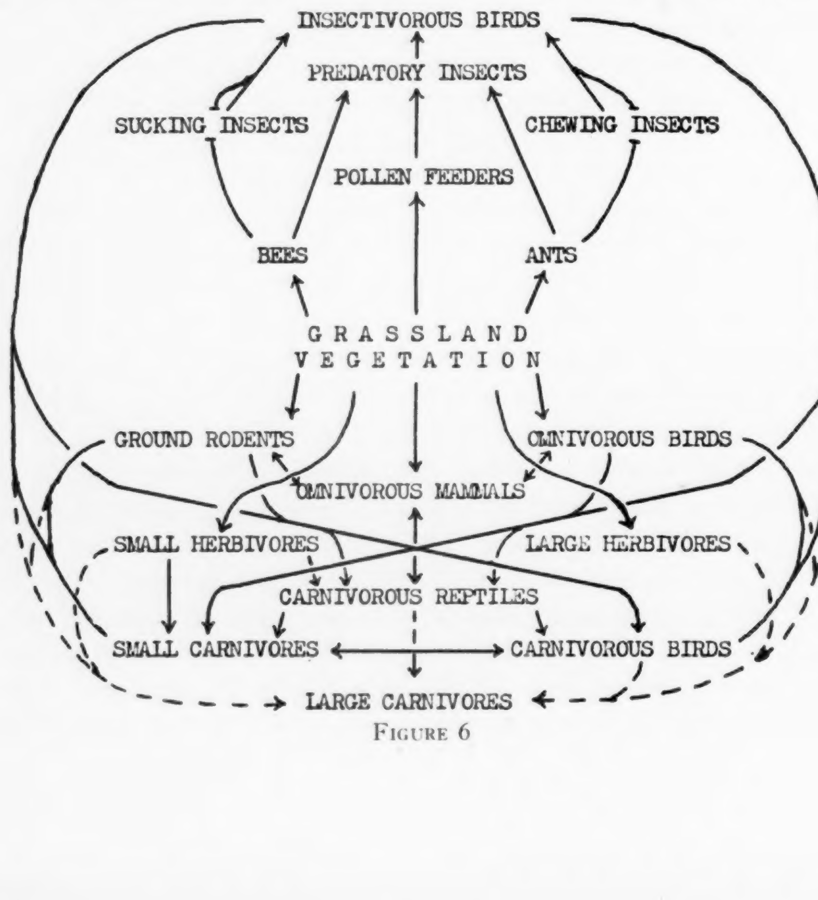

Figure 6

a food-chain diagram (see Fig. 6). In examining this "chain" of ecological events several items should be noted: certain components of the community are much more closely interrelated among themselves than are others: the insects, phytophagous and insectivorous, have many more coactions among themselves than they do with any other of the associated animals. Again, insectivorous birds and such large herbivors as the bison and antelope occupy niches which are themselves without direct contact. However, both are dependent upon the dominant grasses for their ultimate food supply, the bison and antelope directly, and the insectivors much less directly; both of these groups supply the predatory niche occupied by the larger carnivors. The birds, together with the smaller herbivorous rodents and lagomorphs, supply the smaller carnivors (hawks, skunks, snakes, etc.) with food. The phytophagous insect-predaceous insect-insectivorous bird-small predator links in the chain have, therefore, but little linkage with the large herbivor-large predator links, although both are related. In general, the approximate time elapsing during the cycle "from vegetation to predator" is approximately the same in both cases.

VARIATION WITHIN THE BIOME

As was pointed out in a previous section, the plant dominants of the prairie-plains are present throughout a wide east-west range, but in most cases are limited by moisture conditions to given physiographic levels: plants of the uplands in the east are found on sloping prairie areas further west, and finally are found in the far western parts of the grassland only in low, subclimax and non-climatic (edaphic) wet lowlands and ravines. But few of the major dominants extend throughout the entire breadth of the grassland; in the case of the predominants, particularly the mammals, there is much more homogeneity. The more prominent mammals which range throughout the biome, and hence bind it into an ecologic unit, are the bison, antelope, wolf, badger, and the two jackrabbits. Other forms, while taxonomically different in the four divisions, are certainly represented by other ecologically equivalent and frequently closely related forms, lending further homogeneity to the structure of the biome. The mores characteristics of the mammals of the grassland have been discussed in connection with the tall-grass prairie.

The climax grassland, as considered in this paper and as evidenced by the observations cited and recorded, constitute what has been designated the *Andropogon-Bouteloua-Bison-Canis* (GRASSLAND) BIOME. Within this biome or biotic formation three associations have been recognized: climax subdivisions of this larger community, based on the distribution of the areas of dominance of the dominants and predominants. The data, criteria, and analytical tables for each of these associations have been included in the pertinent parts of the text. The extent and composition of the associations have been determined on the basis of their climax stands, although within these

associations, but for the most part not considered in this study, are included the subclimax and seral stages (associes) which also make up, but which do not characterize, an association. Certain areas within any association may be found to be lacking some forms which are characteristic of the community as whole; in some cases these deleted forms are replaced by other, ecologically equivalent forms as has been mentioned. However, being characteristic of the major portion of the community, they may be considered as typical of it, and they are to be included in the abstract concept of the community which is realized in the more typical concrete stands of the community. Extensive areas having important deletions or additions of influential forms are designated as faciations (facies); these may be expressed as

$$\left.\begin{array}{l}\text{The typical community}\\ \quad+\text{ added forms}\\ \quad-\text{ deleted forms}\end{array}\right\}\text{faciation}$$

The grassland-prairie of Illinois, eastern Iowa, eastern Missouri, southern Wisconsin, and western Indiana, frequently termed the "Illinois" prairie in this study, has been shown previously by various authors to be a community which is a subclimax to the forest of the region. Its climate, as has been shown in the second section, is not that typical of the prairie and grassland region as a whole, but is rather of the forest type. However, the ecological structure of the community occupying this area is identical with that of the true (tall-grass) prairie further west, and many of the same dominants, predominants, and influents are found there. Because of the similarity and affiliation to the prairie community type in all respects save that of climax stability, these eastern prairies may be considered as a faciation of the tall-grass association. It is quite evident that this "Illinois" prairie was at one time the climax community for at least the area in which it is now found and, as is evidenced by the "oak openings," "barrens," and other relic spots throughout northern Indiana and southern Michigan, probably extended somewhat further. On the basis of pollen analysis studies Sears (1932) gave this time as about 3000 years ago for Ohio. At the present time this community should be considered as postclimax prairie, being held in a subclimax stage in a deciduous forest succession by edaphic factors. However, this in no way invalidates the view that this portion of the grass-covered area is ecologically related to the remainder: communities are the result of, and occupy those areas characterized by, certain complexes of environmental conditions. If these environmental conditions can be changed by biotic reaction between the biota and the habitat, the community will be succeeded by another, and will be considered as being seral in that locality. On the other hand, if the conditions of the habitat are such that the components of this community are not only well adapted to them but are able to reproduce and maintain themselves as ecologically important forms over long periods, are able to exclude invaders from attaining any degree of

TABLE 7. MAMMALS OF THE GRASSLAND BIOME

Scientific Name	Common Name	Tall Grass Prairie				Mixed Grass Prairie			Short Grass Plains			
		E	N	C	S	N	C	S	N	C	S	
Bison b. bison	Bison	x	x	x	x	x	x	x	x	x	x	Binding Predominants
Antilocapra a. americana	Pronghorn Antelope		x	x	x	x	x	x	x	x	x	
Canis nubilis	Wolf	x	x	x	x	x	x	x	x	x	x	
C. rufus (incl. *frustror*)	"				x			x				
Mustela vison letifera	Badger	x		x	x		x	x		x	x	
M. v. lacustris	"		x			x			x			
Lepus californicus melanotis	Black-tailed Jack Rabbit			x	x		x	x		x	x	
L. townsendi campanius	White-tailed Jack Rabbit		x	x		x	x		x	x		
Sylvilagus floridanus mearnsi	Cottontail	x		x								
S. f. alacer	"				x			x				
S. f. similis	"		x	x		x	x		x	x		
S. audubonii baileyi	"						x			x		
S. a. neomexicanus	"							x			x	
S. nuttalli grangeri	"								x			
Citellus t. tridecemlineatus	13-lined ground squirrel	x	x	x	x	x	x		x			
C. t. badius	"				x							
C. t. pallidus	"					x	x	x	x	x	x	
C. t. texensis	"							x				
Peromyscus leucopus noveboracensis	White-footed Mouse	x		x								Binding Genera
P. l. tornillo	"										x	
P. maniculatus nebrascensis	"						x	x		x	x	
P. m. bairdii	"	x	x	x	x							
P. m. osgoodi	"								x	x	x	
Mephitus hudsonica	Skunk		x			x	x		x	x		
M. mesomelas avia	"	x										
Spilogale interupta	"			x	x		x	x				
M. m. varians	"			x	x		x	x		x	x	
Thomomys talpoides rufescens	Pocket Gopher		x			x						
T. t. talpoides	"								x			
Geomys bursarius	"	x	x	x	x	x	x					
G. leutescens	"									x	x	
Microtus ochrogaster	Prairie Meadow Mouse			x	x		x	x				
M. haydenii	" (Vole)									x		
M. minor	"		x			x			x			
Canis latrans	Coyote	x				x			x			
C. n. nebrascensis	"					x	x		x	x		
C. n. texensis	"							x			x	
Mustela l. longicauda	Long-tailed Weasel					x	x		x	x		
Vulpes v. velox	Kit Fox					x	x	x	x	x	x	
V. v. hebes	Prairie Fox								x			
Cynomys l. ludovicianus	Prairie-Dog						x	x		x	x	
Citellus richardsonii	Richardson Ground Squirrel					x			x			
Perognathus h. hispidus	Pocket Mouse										x	
P. h. paradoxus	"					x	x	x	x	x	x	
P. flavescens flavescens	"									x	x	
P. flavus flavus	"									x	x	
Mustela nigripes	Black-footed Ferret								x	x	x	

NOTE: E, N, C, and S refer, respectively, to the Eastern, Northern, Central, and Southern Faciations of the three associations of the biome. Except in the case of the "binding predominants," species grouped between horizontal ruled lines are considered to be ecologically equivalent species.

dominance in the area occupied by the community, and do not change the habitat by their reactions with it so as to make the environmental conditions unsuitable for the named functions, the community may be termed a climax association. In both instances the community may be the same in all respects save that of climax stability.

Structure of the Biome

The biome, its three associations, and the one affiliated postclimax associes, as recognized on the basis of the area of dominance, biotic composition, and climate, are summarized here only in outline form. Further discussion may be found in the pertinent earlier sections of this study. In this outline the two tall-grass prairie communities, upon which more attention was centered, receive more attention and space than do the other two communities of the biome. Further investigation is necessary before the following outline of the structure of the biome can be made complete.

Andropogon-Bouteloua-Bison-Canis (Grassland) Biome

"Prairiengebiet (Steppen Nordamerikas)." Grisebach, 1872. Veg. d. Erde.
"Prairie Province." Pound and Clements, 1898a, 1900.
"Grassland." Livingston and Shreve, 1921.
"The Grassland Climax: *Stipa-Bouteloua* Formation." Clements, 1920, p. 114.
"*Stipa-Bouteloua-Antilocapra-Bison* Formation." Bird, 1930.
"Grassland Climax (*Stipa-Koeleria* Formation)." Hendrickson, 1930, p. 153.
"Amerikanische Prärie; Duriherbosa; Hartwiesen." Rübel, 1930.
"Prärien: Büffel-Jäger Hauptkulturgebiet." Enzyklopädie d. Erdkunde.
"Grasslands." Shelford and Hanson, 1936, p. 149.
"The Grasslands Formation (Grass-Bison Biome)." Weese, 1938, p. 688.
"The North American Grassland: *Stipa-Antilocapra* Biotic Formation (Biome)." Clements and Shelford, 1939, p. 251.

Range: see map, Figure 7.

Binding dominants: *Andropogon scoparius, Bouteloua gracilis,* and (regionally) *Koeleria cristata.* Equivalent dominants in the following principal genera: *Agropyron, Bouteloua, Stipa.*

Binding predominants:[4] Bison, pronghorn antelope, buffalo wolf, badgers,[4] white- and black-tailed jackrabbits, cottontails,[4] 13-lined ground squirrels,[4] white-footed mice,[4] skunks,[4] pocket gophers,[4] voles.[4]

Cooper's hawk, ferruginous rough-leg, eastern sparrow hawk, scissor-tailed flycatcher (s. & c.), bobwhite, eastern meadowlark, horned larks,[5] dickcissel, greater prairie chicken, upland plover, lark bunting, McCown's and chestnut-collared longspurs, Brewer's blackbird, American raven,

[4] The species, indicated by this figure are represented by several species/subspecies in different areas; see table 7.

[5] The horned larks are represented by two species, the prairie and the desert forms; these are indicated as additions in parentheses in the accounts for the various prairie regions. The common names used are those of the A. O. U. checklist, and are reprinted in the Naturalist's Guide, pp. 743-758; accordingly the scientific names of the birds are omitted.

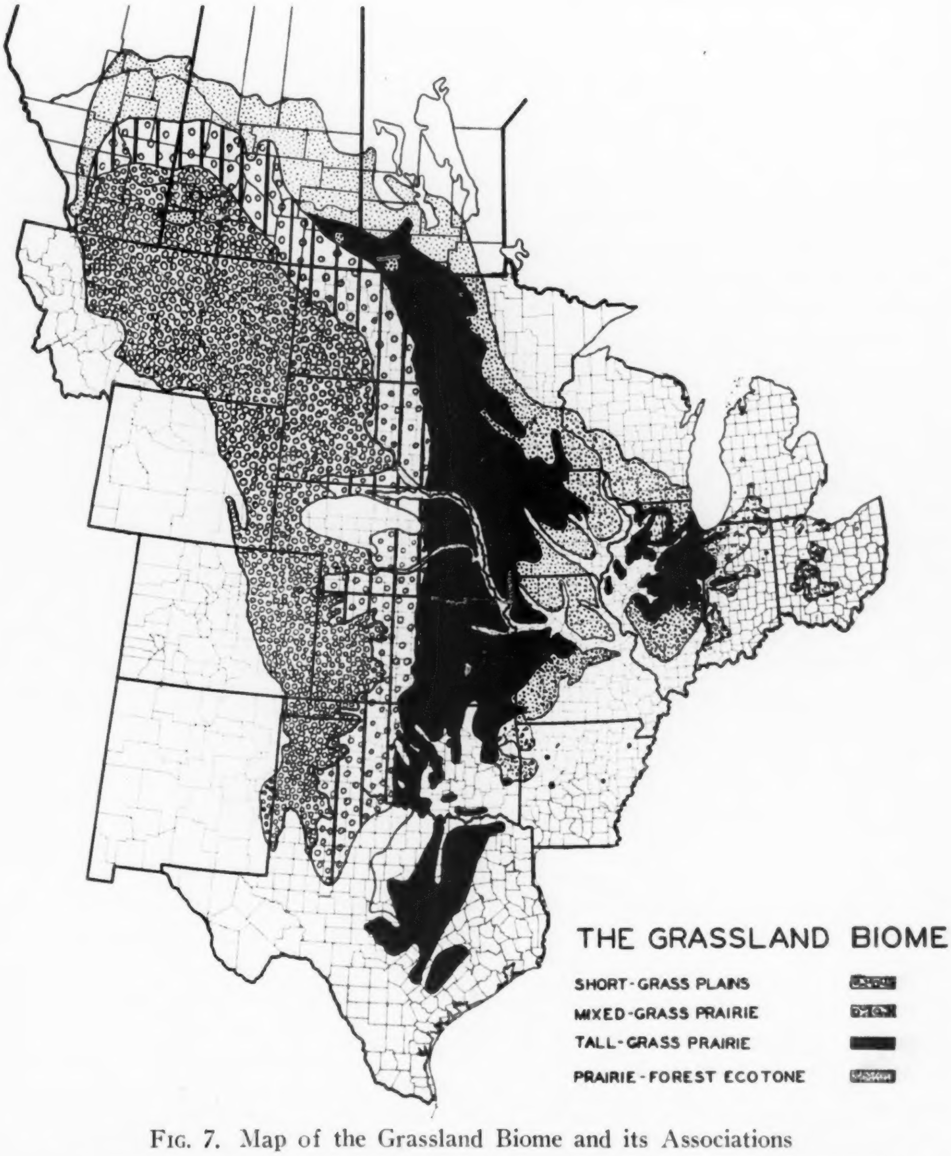

FIG. 7. Map of the Grassland Biome and its Associations

This map was prepared as a compilation of personal observation; of maps presented in the papers of Leopold (1931: north-central United States), Vestal (1931: Illinois), Deam (1929: Indiana), Shimek (1911: Iowa), Ewing (1924: Minnesota), Bird (1930: Canada parklands), Weaver and Fitzpatrick (1934: central prairies), Tharp (1926: Texas), Bray (1901, 1903: Texas), Veatch (1928: Michigan), Sears (1926: Ohio), Pound and Clements (1900: entire area), Aikman (1926: Nebraska; 1935: mixed-grass area), and Transeau (1935: "the prairie peninsula"); and of information obtained through personal communication with A. O. Weese, P. B. Sears, J. M. Aikman, C. C. Deam, C. W. Thornthwaite, K. M. King, and P. G. Phillips.

eastern crow, Sennett's nighthawk, prairie sharp-tailed hawk, western grasshopper sparrow, western mourning dove.

Bufo cognatus, B. woodhousii (toads), *Pituophis s. sayi* (bull snake), *Thamnophis r. radix* (garter snake), *Crotalus confluentus* (prairie rattler), *Terrepene ornata* (box tortoise).

dominance in the area occupied by the community, and do not change the habitat by their reactions with it so as to make the environmental conditions unsuitable for the named functions, the community may be termed a climax association. In both instances the community may be the same in all respects save that of climax stability.

Structure of the Biome

The biome, its three associations, and the one affiliated postclimax associes, as recognized on the basis of the area of dominance, biotic composition, and climate, are summarized here only in outline form. Further discussion may be found in the pertinent earlier sections of this study. In this outline the two tall-grass prairie communities, upon which more attention was centered, receive more attention and space than do the other two communities of the biome. Further investigation is necessary before the following outline of the structure of the biome can be made complete.

Andropogon-Bouteloua-Bison-Canis (Grassland) Biome

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"Grassland Climax (*Stipa-Koeleria* Formation)." Hendrickson, 1930, p. 153.
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"Prärien: Büffel-Jäger Hauptkulturgebiet." Enzyklopädie d. Erdkunde.
"Grasslands." Shelford and Hanson, 1936, p. 149.
"The Grasslands Formation (Grass-Bison Biome)." Weese, 1938, p. 688.
"The North American Grassland: *Stipa-Antilocapra* Biotic Formation (Biome)." Clements and Shelford, 1939, p. 251.

Range: see map, Figure 7.

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Binding predominants:[4] Bison, pronghorn antelope, buffalo wolf, badgers,[4] white- and black-tailed jackrabbits, cottontails,[4] 13-lined ground squirrels,[4] white-footed mice,[4] skunks,[4] pocket gophers,[4] voles.[4]

Cooper's hawk, ferruginous rough-leg, eastern sparrow hawk, scissor-tailed flycatcher (s. & c.), bobwhite, eastern meadowlark, horned larks,[5] dickcissel, greater prairie chicken, upland plover, lark bunting, McCown's and chestnut-collared longspurs, Brewer's blackbird, American raven,

[4] The species, indicated by this figure are represented by several species/subspecies in different areas; see table 7.

[5] The horned larks are represented by two species, the prairie and the desert forms; these are indicated as additions in parentheses in the accounts for the various prairie regions. The common names used are those of the A. O. U. checklist, and are reprinted in the Naturalist's Guide, pp. 743-758; accordingly the scientific names of the birds are omitted.

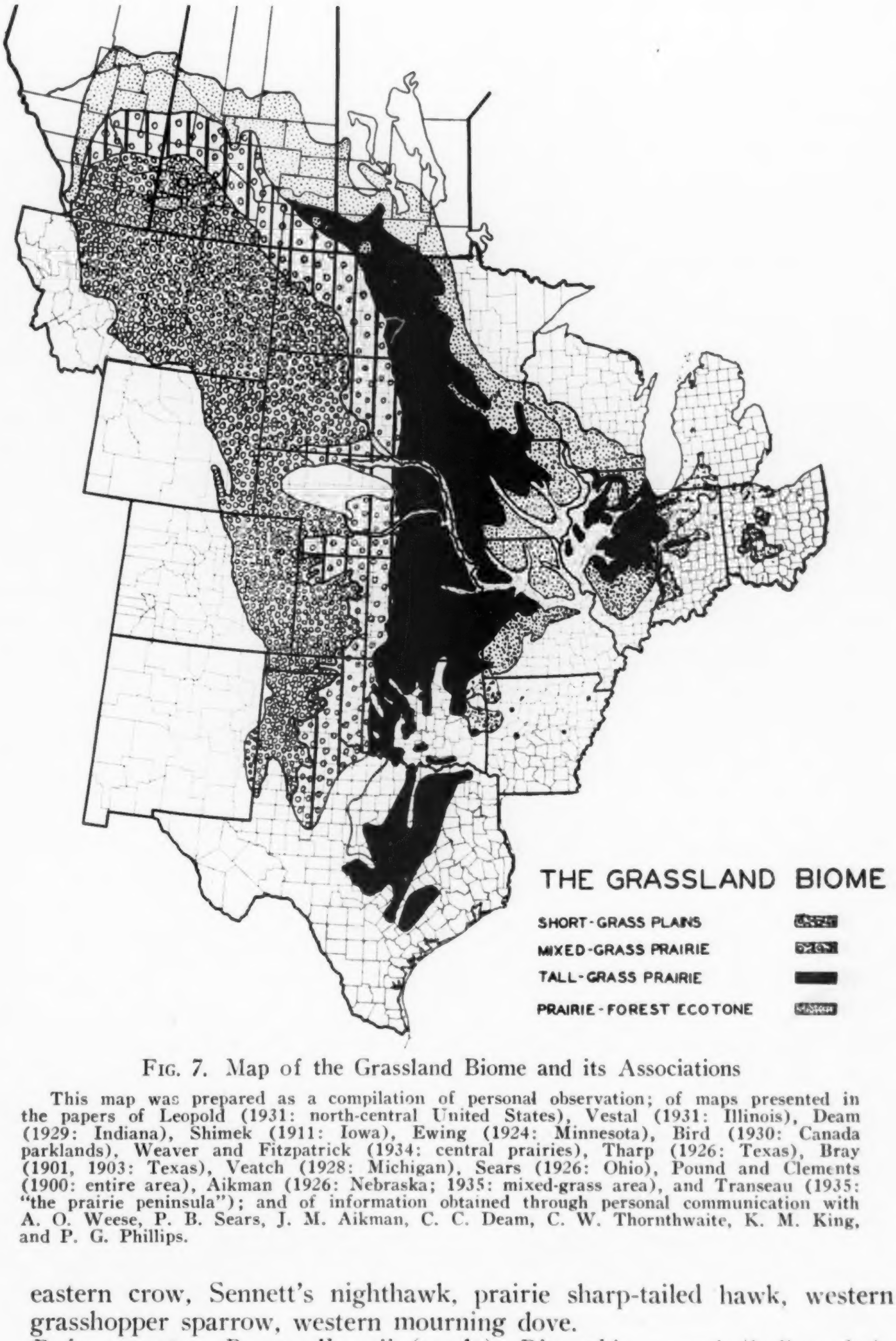

FIG. 7. Map of the Grassland Biome and its Associations

This map was prepared as a compilation of personal observation; of maps presented in the papers of Leopold (1931: north-central United States), Vestal (1931: Illinois), Deam (1929: Indiana), Shimek (1911: Iowa), Ewing (1924: Minnesota), Bird (1930: Canada parklands), Weaver and Fitzpatrick (1934: central prairies), Tharp (1926: Texas), Bray (1901, 1903: Texas), Veatch (1928: Michigan), Sears (1926: Ohio), Pound and Clements (1900: entire area), Aikman (1926: Nebraska; 1935: mixed-grass area), and Transeau (1935: "the prairie peninsula"); and of information obtained through personal communication with A. O. Weese, P. B. Sears, J. M. Aikman, C. C. Deam, C. W. Thornthwaite, K. M. King, and P. G. Phillips.

eastern crow, Sennett's nighthawk, prairie sharp-tailed hawk, western grasshopper sparrow, western mourning dove.

Bufo cognatus, B. woodhousii (toads), *Pituophis s. sayi* (bull snake), *Thamnophis r. radix* (garter snake), *Crotalus confluentus* (prairie rattler), *Terrepene ornata* (box tortoise).

Andropogon-Bison-Canis (Tall-Grass Prairie) Association

"Die Missouri-Prairieregion." Drude, 1890.
"Prairie-Provinz, Prairiegras-Formation." Engler, 1892, Vers. einer Entwg. 2, p. 334.
"Prairie Grass Formation." Pound and Clements, 1900, p. 348.
"Blue stem Formation." Pound and Clements, 1900, p. 355.
"Prairie Grass Formation." Thornber, 1901.
"Prairie region of the Temperate Zone." Clements, 1904.
"Grass-Steppe (Prairie)." Warming, 1909.
"Prairie Region." Harshberger, 1911, p. 516.
"Xerophytic Prairie Grassland Association." Vestal, 1914b.
"Mesophytic Prairie Grassland Association." Vestal, 1914b.
"Upland Prairie Association." Adams, 1915a.
"*Stipa-Agropyrum-Poion.*" Clements, 1916, p. 180.
"*Stipa-Koeleria* Association." Clements, 1920, p. 121.
"*Andropogon furcatus* Association." Sampson, 1921.
"Prairie Community." Dice, 1923.
"True Prairie (*Stipa-Koeleria* Association)." Hensel, 1923.
"Prairie Grass Associes." Ewing, 1924.
"Tall Grass (Prairie Grasslands)." Shantz and Zon, 1924, p. 16.
"Tall Grass or *Andropogon* Prairie." Petry, Nat. Guide, p. 549.
"*Andropogon furcatus* Association." Schaffner, 1926, p. 50.
"*Andropogon-Stipa* Association." Tharp, 1926.
"*Andropogon scoparius-Bouteloua curtipendula* Community." Braun, 1928.
"*Andropogon* Prairie." Braun-Blanquet, 1928.
"Long Grass Grassland." Miller and Parkin, 1928, Geogr. of No. America.
"*Stipa-Koeleria* (True Prairie) Association." Clements, 1929.
"*Agropyron-Microtus* Associes." Bird, 1930.
"*Stipa spartea-Andropogon* Association." Hendrickson, 1930.
"High Prairie." Steiger, 1930.
"*Andropogon* Associes." Bruner, 1931.
"*Stipa-Koeleria* Association." Bruner, 1931.
"*Andropogon-Bison-Canis* Association." Carpenter, 1934.
"The Prairie." Weaver and Fitzpatrick, 1934.
"Prairie Peninsula." Transeau, 1935.
"*Andropogon scoparius-Panicum oligosanthes* Lociation." Carpenter, 1935b.
"True Prairie." Shelford and Hanson, 1936, p. 149.
"*Andropogon furcatus* Climax Prairie Association." Little, 1938, p. 562.
"Tall Grass (Prairie Grassland)." Shantz, 1938, p. 843.
"Bluejoint-Switchgrass Association." Blair, 1938, p. 493.
"*Andropogon scoparius-Panicum oligosanthes* Community." Carpenter, 1939a.
"True Prairie." Clements and Shelford, 1939, p. 269.

Range: see map, Figure 7.

Binding dominants:

High Prairie: *Agropyron repens, Bouteloua gracilis, B. curtipendula, Andropogon scoparius, Poa pratensis, Sorghastrum nutans.*

Sloping Prairie: *Koeleria cristata, Poa pratensis, Sorghastrum nutans, Andropogon furcatus, Stipa spartea.*

Low Prairie: *Andropogon furcatus, Agrostis alba, Spartina Michauxiana, Panicum virgatum, Poa pratensis, Sorghastrum nutans.*

Binding predominants:

+ (prairie horned lark), bobolink, eastern savannah sparrow, eastern red-tailed hawk, Krider's hawk, long-billed curlew.

Binding seasonal subdominants:

Prevernal Sociation: *Antennaria campestris.*

Vernal Sociation: *Rudbeckia hirta, Lithospermum angustifolium, L. canescens, Anemone cylindrica, Baptisia bracteata.*

Estival-Serotinal Sociations: *Erigeron ramosus, Petalostemon purpureum, Rudbeckia hirta, Amorpha canescens, Acerates viridiflora, Lephachys columnaris, Œnothera serrulata, Apocynum cannabinum.*

Autumnal Sociation: *Solidago nemoralis, S. missouriensis, S. rigida, Helianthus scaberrimus, Aster multiflorus, Liatris punctata.*

Binding influents:

Melanoplus bivittatus, Eugnathodes abdominalis, Scolops spurcus, Œcanthus nigricornus sspp., *Campylenchia latipes, Adelphocoris rapidus, Sinea diadema, Platymetopius frontalis, Argiope trifasciata, Euschistus variolarius, Diabrotica 12-punctata, Syrbula admirabilis, Hippodamia convergens, Epicauta pennsylvanica, Stictocephala lutea, Orphulella speciosa, Xerophloea viridis, Ageneotettix deorum, Gryllus assimilis, Deltocephalus configuratus, Dissosteira carolina, Melanoplus neomexicanus atlanis, M. femur-rubrum, Deltocephalus inimicus, Chortophaga viridifasciata, Opeia obscura, Melanoplus packardi, M. confusus.*

THE EASTERN ("POST CLIMAX") FACIATION

Andropogon-Silphium-Citellus ("ILLINOIS PRAIRIE") ASSOCIES

(being a post-climax relic of this biome, but preclimax to the Deciduous Forest Biome.)

"Prairie." Cowles, 1901, Geogr. Soc. Chi. Bull. 2.
"Prairie Grass Formation." Harshberger, 1911, p. 522.
"High Prairie Association." Shelford, 1913.
"Black Soil Transition Association." Vestal, 1913.
"Prairie Grass Associations." Adams, 1915a.
"Prairie Meadow of the upland." Braun, 1921.
"*Andropogon scoparius-Bouteloua curtipendula* (Xeric) Prairie." Braun, 1928, p. 289.
"*Andropogon furcatus* Prairie with *Silphium terebinthinaceum.*" Braun, 1928, p. 295.
"*Andropogon-Scleria* Meadow." Braun, 1928a.
"*Andropogon furcatus-Silphium terebinthinaceum* Prairie." Braun, 1928a.
"*Lygus-Formica-Microtus* Presocies." Shackleford, 1929.
"Grand Prairie." Vestal, 1931b.
"*Andropogon-Citellus* Associes." Carpenter, 1934.

Range: n. & c. Ill., n.w. Ind., s.w. Wisc., e. Iowa (see Figure 7).

Dominants:

High Prairie: + *Sporobolus heterolepis, Spartina Michauxiana,*[6] *Stipa spartea.*

Sloping Prairie: + *Eleocharis palustris, Spartina Michauxiana,*[6] *Panicum virgatum.*

— *Koeleria cristata,*[6] *Sorghastrum nutans.*

[6] Reference to Chicago region (Cook Co.) but not to the rest of the "Illinois" prairie.

Low Prairie: + *Calamagrostis canadensis, Eleocharis palustris,*[6] *Sporobolus heterolepis.*

Predominants: see Table 7.

Seasonal subdominants:

Prevernal Socies: that characteristic of the association.

Vernal Socies: + *Geum trifolium, Phlox pilosa.*

— *Lithospermum angustifolium.*

Estival-Serotinal Socies: + *Psoralea tenuiflora, Apocynum cannabinum.*

— *Acerates viridiflora, Lephachys columnaris, Œnothera serrulata.*

Autumnal Socies: — *Solidago missouriensis.*

Influents:[7]

Hippiscus rugosus, Entocoptolopha sordidus, Arphia sulphurea, Neoconocephalus ensiger, Lygus pratensis, Formica pallide-fulva, Chaetocnema confinus, Longitarsus testaceus, Argiope auriantia, Xiphidium strictum, Euschistus variolarius, Melanoplus differentialis, Tetraopes tetraopthalmus, Epicauta marginata, Scudderia texensis, Botanobia dorsata, Madiza cinerea, Chloropisca glabra, Glyptina sp., *Tomocerus flavescens, Dendrophantes* sp., *Typophorus canellus.*

— *Chortophaga viridifasciata, Opeia obscura, Melanoplus packardi, M. confusus.*

The Northern Faciation of the Tall-Grass Prairie

Range: s.w. Man., N. Dak., n. S. Dak.

Dominants:

High Prairie: + *Koeleria cristata, Stipa spartea.*

— *Poa pratensis, Sorghastrum nutans.*

Sloping Prairie: + *Stipa comata, Elymus canadensis, Agropyron Richardsoni.*

— *Koeleria cristata, Poa pratensis, Sorghastrum nutans, Andropogon furcatus, Stipa spartea.*

Low Prairie: + *Stipa spartea, S. comata, Elymus canadensis.*

— *Agrostis alba, Spartina Michauxiana, Panicum virgatum, Poa pratensis, Sorghastrum nutans.*

Predominants: — Dickcissel, *Terrapene ornata;* see Table 7.

Seasonal subdominants:

Prevernal Sociation: that characteristic of the association.

Vernal Sociation: — *Baptisia bracteata.*

Estival-Serotinal Sociation: + *Petalostemum candidum, Rosa pratincola, Lilium philadelphicum.*

— *Lepachys columnaris, Œnothera serrulata, Apocynum cannabinum.*

Autumnal Sociation: that characteristic of the association.

Influents:[7]

+ *Melanoplus gladstoni, M. angustipennis, M. perplexa, M. infantilis, M. bruneri, M. m. mexicana, Spharagemon collare, Trimerotropis monticola, T. campestris, Arphia pseudonietana, A. conspersa, Gomphocerus clavatus, Camnula pelucida, Chloealtis conspersa, Neopodismopsis abdominalis, Pardalophora apiculata, Xanthippus corallipes, Encoptolophus costalis, Metator pardelinus, Hypochlora alba, Systoechus vulgaris, Epicauta* spp., *Macrobasis* sp., *Lytta* sp., *Laccocera vittipennis, Drikaneura moli, Eustilbus apicolis, Lasius brevicornis, Myrmica scabrinoides, Homaemus aenifrons, Hylemyia elicrura, Melanochila surda.*

[6] Refers to Chicago region (Cook Co.) but not to the rest of the "Illinois" prairie.

[7] See also under influents of the central prairie.

— *Eugnathodes abdominalis, Scolops spurcus, Campylenchia latipes, Adelphocoris rapidus, Sinea diadema, Argiope trifasciata, Euschistus variolarius, Diabrotica 12-punctata, Syrbula admirabilis, Hippodamia convergens, Stictocephala lutea, Xerophloea viridis, Dissosteira carolina, Deltocephalus inimicus, Platymetopius frontalis.*

The Central Tall-Grass Prairie ("Typical Faciation")

Range: s. S. Dak., Nebr., n. Kans., s.w. Minn., w. Iowa.
Dominants:
High Prairie: + *Panicum virgatum, P. Scribnerianum, Bulbilis dactyloides, Bouteloua hirsuta, Sorghastrum nutans.*
Sloping Prairie: + *Schedonnardus paniculatus, Sporobolus heterolepis, S. cryptandrus, Bouteloua curtipendula, B. gracilis, B. hirsuta, Andropogon scoparius.*
Low Prairie: + *Elymus canadensis, Sorghastrum avenaceum, Koeleria cristata, Panicum Scribnerianum, Bouteloua curtipendula, Andropogon scoparius, Agropyron pseudorepens.*
Predominants: see Table 7.
Seasonal subdominants:
Prevernal Sociation: + *Anemone caroliniana, Draba caroliniana, Capsella Bursa-pastoris, Androsace occidentalis.*
Vernal Sociation: + *Castillija sessiflora, Œnothera serrulata, Anemone caroliniana.*
— *Anemone cylindrica, Lithospermum canescens.*
Estival-Serotinal Sociation: + *Verbena stricta, Plantago Purshii.*
— *Acerates viridiflora, Apocynum cannabinum.*
Autumnal Sociation: that of the association.
Influents:
Central Area: + *Spharagemon aequale, Dactylotum pictum, Brachystola magna, Philbostroma* sp., *Nachyrachis* sp., *Argynnis* sp., *Apatelia* sp., *Basilarchia* sp., *Chrysophanus* sp., *Coelnonympha* sp., *Colias* sp., *Lycaena* sp., *Thanaos* sp., *Eleodes obsoleta, E. opaca, E. tricostata, Silpha ramosua, Harpalus craticus, Arethaea aracilipes constricta.*
— *Syrbula admirabilis, Stictocephala lutea.*
Eastern and Central Faciations: + *Euaresta bella, Nodonota convexa, Coenosia lata, Phyliomyia indecora, Sphaerophoria cylindrica, Diabrotica longicornis, Chauliognathus pennsylvanicus, Triphleps insidiosus, Mesograma marginata, Alydus conspersus, Pachybrachys luridus, Languria mozardi, Ormensis pruinosis.*
Central and Northern Faciations: + *Melanoplus dawsonii* and *keeleri luridus, Trachyrachis (Mestobregma) kiowa kiowa.*
Central and Southern Faciations: + *Nabis subcoleoptratus, Ortholomus scolopax, Adelphocoris viridis, Peribalus limbolarius, Chlorotettix unicolor, Bruchomorpha dorsata, Nabis ferus, Mermiria maculipennis macclungi, Platymetopius cinereus, Graphops varians, Phalacrus politus, Collops 4-maculatus, Hadrotettix trifasciata.*

The Southern Faciation of the Tall-Grass Prairie

Range: S. Kans., w.c. Okla., n.c. Texas.
Dominants:
High Prairie: + *Stipa leucotricha, Andropogon saccharoides, A. tener, A. ternarius.*
— *Poa pratensis, Sorghastrum nutans.*

Sloping Prairie: + *Andropogon saccharoides, Panicum oligosanthes.*
— *Koeleria cristata, Poa pratensis, Sorghastrum nutans.*
Low Prairie: — *Agrostis alba, Spartina Michauxiana, Panicum virgatum, Poa pratensis, Sorghastrum nutans.*

Predominants: see Table 7.

Seasonal subdominants:

Prevernal Sociation: that of the association.

Vernal Sociation: + *Penstemon cobaea, Indigofera leptosepala, Verbena bipinnatifida, Lepidium apetalum.*
— *Anemone cylindrica, Lithospermum canescens, Rudbeckia hirta.*

Estival-Serotinal Sociation: + *Asclepias verticillata, Asclepiodora viridis, Psoralea cuspidata, Krameria secundiflora, Houstonia angustifolia, Silphium lanceolatum,* and others.

Autumnal Sociation: — *Solidago missouriensis.*

Influents:[8]

+ *Typophorus canellus, Draeculocephala mollipes, D. minor, Gypona octileata, G. miliaris, Xerophloea major, Deltocephalus weedi, D. weedi, D. obtectus, D. compactus, Euscellis bicolor, Phlepsius irroratus, Thamnotettix nigrifrons, T. colonus, T. inornatus, Strongyloris stygicus, Chaetocnema denticulata, Ortholomus jamaicensis, Mordellistena lutea, Haltica bimarginata, Onychobaris pectorosa, Epitrix brevis, Mormidea lugens, Idiocerus crataegi, Mecidea longula, Mermiria maculipennis, M. neomexicana macclungi, Cymus viricens, Deltocephalus sandersi, Melanoplus packardi, M. confusus, M. foedus, Hesperotettix v. viridis, H. v. pratensis, H. speciosus, Arphia simplex, Aulocara ellioti, Pardalophora saussurei, Hippiscus rugosus, Eritettix simplex, Diapheromera veliei, Neoconocephalus robustus, Pachybrachys morosus, Pleurostychus convexicaulis, Mitostylus tenuis, Systena hudsonias, Nodonota clypealis, Altica foliacea, Pseudoleria pectinata, Empoasca viridescens, Campylenchia latipes, Galgupha nitiduloides, Andrenidae.*

Andropogon-Bouteloua-Bison-Antilocapra (Mixed-Grass Prairie-Plains Association

Synonomy: see p. 645.

Range: see map, Fig. 7.

Dominants: *Bouteloua gracilis, B. hirsuta, Andropogon scoparius, Bulbilis dactyloides.*

Predominants: + Kitfox, prairie-dog, Richardson ground squirrel, long-tailed weasel, pocket mouse, blackfooted ferret.
+ (prairie and desert horned larks), eastern savannah sparrow, eastern red-tailed hawk, Krider's hawk, western vesper sparrow, Howell's nighthawk, longbilled curlew, Sprague's pipit, western burrowing owl, western lark sparrow.
+ *Phrynosoma cornutum* (horned toad).

Northern Faciation of the Mixed-Grass Association

+ *Koeleria cristata, Stipa spartea, S. comata,* Richardson ground squirrel, pocket gophers; see Table 7.
— *Bulbilis dactyloides,* scissor-tailed flycatcher, prairie-dog, *Terrapene carolina;* see Table 7.

Range: Man., N. Dak., n. S. Dak.

[8] See also under influents of the central prairie.

Bouteloua-Bulbilis-Bison-Antilocapra (SHORT-GRASS PLAINS) ASSOCIATION
Synonomy: see p. 649.
Range: see map, Fig. 7.
Dominants: *Bouteloua gracilis, Bulbilis dactyloides.*
Predominants: + Long-tailed weasel, coyote, kitfox, prairie fox, prairie-dog, pocket mouse, black-footed ferret.
+ (desert horned lark), western vesper sparrow, Howell's nighthawk, western burrowing owl, western lark sparrow, western field sparrow.
+ *Phrynosoma cornutum* (horned toad).

FACIATIONS:

1. — *Bulbilis dactyloides* (= *Bouteloua gracilis* CONSOCIATION)
   Range: e. Wyo., c. & e. Mont., s.w. Sask., s.e. Alta.
2. + *Stipa comata,* Saskatchewan pocket-gopher, Richardson ground squirrel, Black Hills cottontail.
   — *Bulbilis dactyloides,* prairie-dog, plains pocket mouse, *Terrapene ornata.*
   Range: n. & c. S. Dak., c. & w. N. Dak., n.e. Mont., s.w. Sask.
3. + *Agropyron Smithii.*
   Range: c., s.w., & w. S. Dak.
4. + Black-tailed jackrabbit, New Mexico cottontail, scissor-tailed flycatcher.
   — Buffalo wolf, long-tailed weasel, badger.
   Range: Oklahoma and Texas Panhandles.

SUMMARY

The grassland of North America constitutes a biotic community which is typical of continental climates throughout the world. This study is an attempt to treat this biotic community in monographic form, using as source material previous descriptions of the area and personal observations. The regional boundaries of this community, while dependent upon climatic factors working through edaphic conditions, have changed during the major historic shifts in climate.

Three climax grassland types or associations are recognized within the *Andropogon-Bouteloua-Bison-Canis* (GRASSLAND) BIOME: the *Andropogon-Bison-Canis* (TALL-GRASS PRAIRIE) ASSOCIATION, the *Andropogon-Bouteloua-Bison-Antilocapra* (MIXED-GRASS PRAIRIE-PLAINS) ASSOCIATION, and the *Bouteloua-Bulbilis-Bison-Antilocapra* (SHORT-GRASS PLAINS) ASSOCIATION. Of the three, the first has received the greatest amount of study.

A study of the distribution of the dominant components of the vegetation from an analysis of the published observations on the ecology and life histories of the dominants, showed that species which were characteristic of high areas in the more humid east were found to be characteristic of sloping areas further west, and restricted to low areas in the westernmost portion of their dominance range, thus agreeing with the observations of Schaffner (1926).

The faciations of the prairie were determined on the basis of the geographic distribution of the areas of dominance of the dominants and predomi-

nants at each of the physiographic levels mentioned above. The most typical stands of the prairie were in the area centering about Nebraska, since in this region were present the majority of the prairie dominants. Northern, southern, and eastern faciations of the prairie were recognized and defined in terms of the dominants and predominants. A portion of the eastern faciation centering about Illinois was considered as a post-climax relic of the prairie association, now subclimax to the deciduous forest biome.

The predominants—mammals and birds—when examined by a method similar to that used for the dominants, showed a greater homogeneity in their areas of predominance throughout the prairie than did the dominants, although the presociation in the extreme northern and southern reaches of the prairie shows slightly different composition from that of the central, typical area. From the available studies on the influents it appears that there is a relatively uniform composition throughout the prairie of many of the lesser forms.

The subdominant plants making up the seasonal sociations of the prairie likewise showed a marked similarity in the various areas which have been studied, showing that a given seasonal sociation is characteristic of the association as a whole, and not of a particular lociation only.

The *Andropogon-Bouteloua-Bison-Antilocapra* (mixed-grass prairie-plains) Association is, in a sense, a relatively broad ecotone or transition between the two other associations of the biome, but nevertheless possesses certain characteristics peculiar to itself; it is an emergent, and as such attains a certain degree of individuality and is sufficiently stable to be considered as of associational rank. While the community has been sufficiently studied to designate its faciations, the dominants appear to be fairly uniform throughout, excepting again the far northern areas.

The *Bouteloua-Bulbilis-Bison-Antilocapra* (short-grass plains) Association is the most xeric of the communities of the biome. It presents a greater number of major faciations as indicated by the dominants than does the prairie, but the animal constituents are remarkably consistent throughout the entire area, except that in the north there is an abrupt transition to a northern faciation characterized by certain predominants.

This study shows that the grassland, as herein defined, constitutes a natural biotic unit of the rank of a biome having throughout a common physiognomy, a constant growth form on the part of the dominants, a similar ecological structure, essentially similar climographic patterns, and a homogeneity of the larger predominant forms in most areas. The study concludes with an outline of the structure of the biome.

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RELIC PRAIRIE AREAS IN CENTRAL WISCONSIN[1]

By

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RELIC PRAIRIE AREAS IN CENTRAL WISCONSIN

INTRODUCTION

One of the persistent problems of the ecologist is the "Prairie Peninsula," the large area of prairie which was present in Illinois, Indiana, Iowa, Missouri, Wisconsin, and with eastward outliers in Ohio, Kentucky, and Tennessee at the time of settlement of the midwest. An excellent, critical summary of the problem is presented by Transeau (1935).

Gleason (1922) postulates a dry warm period following the last glaciation of the midwest. During this period the prairies advanced eastward as far as Ohio and northwestern Pennsylvania, following the retreating coniferous forests. Transeau (1935) states that there is insufficient evidence for an early postglacial xeric period but the evidence points more to a later xeric period. A study of a Wisconsin peat bog by Truman (1937) points to a later postglacial xeric period in Wisconsin, during which two prairie invasions took place. Following this early or later postglacial prairie invasion there was an increase in rainfall accompanied by an extension of deciduous forests westward. When the forests encroached upon the prairie, small communities of prairie plants were left behind in the retreat of the prairie and these relics of the former greater postglacial extent of the prairie persisted until the time of settlement of the midwest. The present paper deals with the prairie flora in central Wisconsin following settlement of this region in the eighteen-fifties. Central Wisconsin is a particularly favorable region for such a study as it is on the fluctuating border between the prairie and the deciduous forest.

The field work during portions of the summers of 1936, 1937, and 1938 was made possible by grants from the Alumni Research Foundation of the University of Wisconsin. Grateful acknowledgment is made to Professor N. C. Fassett for constant help and suggestions during the progress of this study. I am much indebted to my wife Olive S. Thomson for assistance in the field and in the preparation of this report. Through the generous hospitality of Mr. and Mrs. F. N. Hamerstrom, Jr., their home at Necedah was made a center of operations during part of the survey. The distribution of the prairie species in Juneau County was surveyed by Arthur Hoffman, Edgar Riley, Jr., Arthur Oehmcke, and Elton Bussewitz. The survey of distribution in the other counties was made by the writer. Studies on the plant succession in abandoned fields in Juneau County have been reported upon elsewhere.

The portion of Wisconsin which is covered by this study is indicated in Figure 1. The maps showing the distribution of the prairie species are based on the soil surveys of the various counties concerned and on the general soils map of Wisconsin by Whitson (1926). On these maps the dry sandy soils are shown by the stippled area but much of the northern part of Juneau and

FIG. 1. Location of the portion of Wisconsin covered by this study.

Adams Counties and the southern part of Wood County is called "sands and peat undifferentiated" in the soil survey reports. On some of the drier portions of this area the prairie species may occur as noted later. Soil types other than sandy have been omitted. The locations of the prairie relic communities shown on the maps by crosses, at the time of settlement, were determined by examination of reports of surveys made in 1851 by surveyors from the U. S. Land Office at Dubuque, Iowa. These reports are now on file in the Public Land Office, State Capitol Building, Madison, Wisconsin. Of great assistance also was the "General Map of the Native Vegetation of Wisconsin in 1882." Assistance in locating and naming prairie relics in Juneau County was given by Mr. James Blake of Necedah who knows much about

the early settlement of Juneau County. In LaCrosse and Monroe Counties the existing relics are shown on the maps and are mainly located on southwestern bluff slopes. The mapping of the present distribution of the prairie species was done mainly by recognition from a car moving at from fifteen to twenty miles an hour. When a community of prairie plants was seen, the car was stopped and the community examined. Notes were made as to the species present and their relative abundance estimated and collections were frequently made for the Herbarium of the University of Wisconsin. Often the country away from the roadside was examined by leaving the car and walking back into the territory to make notes. The vicinity of relic communities was examined as carefully as time permitted both on foot and with the car. The notes were written in a notebook in the field and later transposed to the distribution maps. The number of dots within each section of each township on the maps indicates the abundance of each species, based on the estimated density of the plants of that species in the section. One dot represents its presence as one or a few plants, two dots represent frequent or fairly common, three dots represent common and four dots represent abundant. Figure 2 shows the roads traveled during the survey. While some of the roads were traveled more than once, the notes were made but once for each section of road so that there is no duplication of observation with consequent massing of any species on any portion of the maps due to such duplication. The notes made during the survey of Juneau County by the above mentioned men in 1936 were reduced to the same scale as those used by the

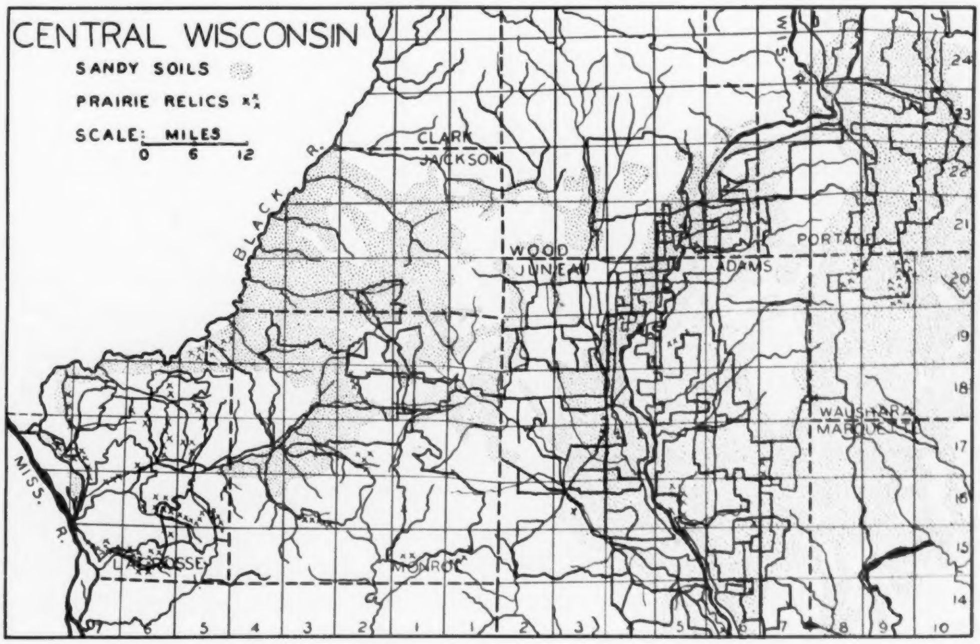

FIG. 2. Roads traveled in central Wisconsin during the survey.

writer in the survey of the other counties. Additional data on the distribution of species of the family Leguminosae were obtained from collections made or examined by Fassett (1939).

In September, 1937, a trip which included most of the sandy areas of the state was taken by Professor Fassett and the writer. During the last week in August, 1938, the writer drove up the valley of the Wisconsin River into Vilas County to determine the distance which the prairie species had traveled northward via this route. The observations made on these trips are embodied in the discussion which follows.

GEOLOGY AND PHYSIOGRAPHY

The basic underlying rock of the counties included in this study is the Cambrian series of sandstones. This rock has contributed most to the surface deposits of the central sand plain of Wisconsin. In southern LaCrosse County, southern Monroe County, and a small portion of southwestern Juneau County the hills are capped with the more resistant Lower Magnesian limestone. The rocks underlying this region slope gently to the southwestward and the topography of the Driftless Area is largely the expression of normal erosion upon these retreating cuestas of sedimentary rock of varying degrees of hardness. Some crags, buttes, and mesas are left in the central plain by the retreat of the escarpment. While most of the area was not covered by ice during glaciation, the glaciers had considerable effect upon it. A portion of northern Wood County was glaciated in an older glaciation than the Wisconsin but left untouched by the Wisconsin stages of glaciation. The Johnstown end moraine of the third Wisconsin substage of the Wisconsin glaciation winds as a gravel and sand ridge with knobs and kettles across southeastern Adams County, western Waushara County, and eastern Portage County. The preglacial Wisconsin River was dammed by the ice at Wisconsin Dells and at the Baraboo Range and the glacial waters formed a large lake which covered most of Adams and Juneau Counties and much of Wood, Jackson, and Monroe Counties. Another arm of the lake was formed in the valley of the Baraboo River, extending up as far as Elroy. Glacial Lake Wisconsin drained westward down the east fork of the Black River from Scranton, Wood County, to Hatfield, Jackson County. The lake did not last long as the beach deposits are slight. Ice rafted erratics show a beach line of 960 feet above sea level at the southern end of the lake and 1000 feet at the northern end. This discrepancy is due to recent tilting up of the land to the northward. Many of the crags existed as islands in the lake as shown by the beach deposits upon them. As soon as the lower outlet to the south through the Dells was opened by the recession of the ice and cutting through of the terminal moraine by the water, the lake was drained and the old course of the river in central Wisconsin resumed. The presence of the crags, buttes, pinnacles, and mesas in the central sand plain in Juneau County and the west-

ern part of Adams County proves that these areas, although covered by much outwash, were unglaciated. The higher terraces in the Black, Mississippi, and Wisconsin Rivers are largely composed of outwash material in which the rivers have since eroded lower channels.

SOILS

The soils in the central Wisconsin counties under consideration are mainly residual from weathering of the Lower Magnesian limestone and the Cambrian sandstones. Wind, water, and glaciation have acted upon some of the material and redeposited it. Extensive areas of peat are found in Wood, Portage, Adams, Juneau, and Jackson Counties, and in northern Monroe County. East of the moraine in Portage, Waushara, Marquette, and Adams Counties are mainly the Coloma soils which are sandy soils derived by glacial reworking of the residual sand which originally covered the area. The original vegetation of this area was largely oaks. Plainfield soils are sandy soils formed by stream and lake action on the residual sands and to some extent in Waushara and Marquette Counties are glacial outwash. A broad portion of Adams County and large areas in northeastern Juneau County, northern Monroe County, and southern Jackson County are covered with Plainfield soils. Pine and oak were the original plants on these soils with possibly some "oak openings." Brice and LaCrosse prairies in LaCrosse County and some of the prairie relics in Juneau and Adams Counties are on these soils. Boone sandy soils are chiefly residual and are more limited in extent. The larger areas occur in Jackson and Juneau Counties. White and Norway pines were the original vegetation but scrub and black oak and jack pine have supplanted them now. The Waukesha sandy loams in Adams and Waushara Counties are important in this study as their original vegetation was prairie. They were derived from outwash and alluvial material with considerable additions of organic matter. Considerable areas of black loamy sands, Dunning sands, which are poorly drained, are present but these are too wet for growth of the prairie plants. On the uplands in Monroe, Juneau, Jackson, and LaCrosse Counties the soils are residual from the Lower Magnesian limestones and are higher in silt. The Baxter silt loams in Juneau and Monroe Counties were forested, but on the Knox silt loams which are residual from shale and sandstone with perhaps some loess "much of the forest is said to have grown up since the county (Monroe) was first settled 60 years ago" (Soil Survey of Monroe County) although this series is now covered with oak-hickory forests. Most of northern Wood County is covered by Colby silt loam and Vesper silt loam which have been derived from earlier glaciations than the Wisconsin. They are mainly poorly drained soils covered with hardwood forest. In LaCrosse and Monroe Counties the prairie relics are mainly on soils mapped as "rough stony land," as they are on the bluff sides. In much of the central sand area the soils maps show "sands and peat undiffer-

entiated" and these areas have not been stippled on the maps accompanying this report. While most of such areas is low, on the sand islands there is a vegetation of oaks, jack pine, and very often some of the prairie species in the undergrowth. Roadsides and dry ditch banks in these areas also provide suitable habitats for the prairie plants.

CLIMATE

The average annual precipitation in the central counties varies from 30 to 33 inches with the greater amount in Monroe and Jackson Counties, and the lesser in western LaCrosse County and northeastern Juneau County. Half of this total comes during May, June, July, and August. Seventy percent comes between April 1 and September 30. June has the heaviest rainfall with 4.1 inches, July has 4 inches, and May 3.9 inches. Precipitation in the winter is light; December, January, and February average 1 to 1.5 inches of rain and melted snow. During the growing season 21 inches of rain are received. Often there are periods of drought of from one to four weeks, occasionally longer; serious droughts occurred four times between 1882 and 1927. The periods of drought on the sandy soils average longer and are more frequent.

The mean annual temperature is slightly lower in Wood, Portage, Adams, Juneau, and eastern Monroe Counties (43 to 44°F.) than in western LaCrosse County (45 to 46°F.). Summer and winter temperatures are correspondingly low. The mean summer temperature is 67 to 68°F. in the former and 70 to 71°F. in the latter. The mean winter temperature is 15 to 16°F. in Wood and Portage Counties, 16 to 17°F. in Juneau, Adams, Monroe, and eastern LaCrosse Counties, and 18 to 19°F. in southwestern LaCrosse County. The average annual minimum temperature recorded at LaCrosse is —20°F. and the average annual maximum temperature recorded at the same station is 97°F. The mean absolute minimum temperature over all the area but western LaCrosse County is —25 to —30°F. The growing season in Wood County, western Portage County, Jackson, Juneau, and Monroe Counties averages 130 to 140 days and is less than in the rest of the area where there may be up to 160 to 170 days without a killing frost as in western LaCrosse County. The date of the last killing frost in spring in western LaCrosse County is before May 1; over most of the area it is between May 10 and May 20, and in the northern part of the area it is between May 20 and June 1. The date of the first killing frost in the fall is between September 10 and 20 in Wood County and northern Juneau County; and between September 20 and 30 over most of the central Wisconsin area but is as late as October 1 to 10 in western LaCrosse County. The growing season is shorter on the low, marshy territory and sandy soils.

PRAIRIE RELICS

Communities of species remaining as relics of a former greater extension of the prairie eastward are important in any study of the prairie at the edge of its range. They may serve as possible "reservoirs of reinfection" in any later invasion, or spread from the relics may be combined with a general invasion from the south or west. A third possibility but less likely is that the plants in these communities may remain stagnant while a general wave of invasion passes over them and beyond in the state.

The various communities here termed "relics" are undoubtedly parts of a former more extensive range of prairie northeastward in the state. While the prairie at the edge in all probability did not form a continuous line of contact, but rather a series of extensive openings among the forested areas at its borders, there must have been considerable prairie in the central sand plain area of Wisconsin at the time of maximum advance of the prairie.

In Adams County there are seven localities where there are relics of prairies. These localities are mentioned either in the 1851 surveyors records or in the 1882 vegetational map and either show communities of prairie plants or still have concentrations of prairie plants near them. A fine relic of Dell Prairie is preserved at T. 14 N., R. 6 E., secs. 10 and 11 (see Fig. 3). Dell Prairie, after which the township is named, is shown on the surveys of 1851 but not on the map of 1882 probably because by that time it was largely under cultivation. Twenty-four species are present on this relic. These are: *Andropogon furcatus, Andropogon scoparius, Stipa spartea, Sorghastrum nutans, Sporobolus heterolepis, Bouteloua hirsuta, Koeleria cristata, Tradescantia canaliculata, Geum triflorum, Lespedeza capitata, Petalostemum purpureum, Petalostemum candidum, Amorpha canescens, Euphorbia corollata, Lithospermum Gmelini, Asclepias tuberosa, Linum sulcatum, Gentiana puberula, Liatris scariosa, Hieracium longipilum, Aster sericeus, Aster multiflorus, Coreopsis palmata,* and *Solidago rigida.* The top 6 to 8 inches of sandy soil at this point are dark with organic matter. Professor A. R. Whitson has advised, however, that there was not sufficient organic matter to differentiate the sandy soil at these relics from the Plainfield series. The organic matter in these sandy soils disintegrates very rapidly and the accumulation of organic matter to produce a prairie soil is inhibited. The cultivation of the relics would also hasten the decomposition, and the prairie areas were among those first cultivated in this region as there was no difficulty in clearing the land. The prairie plants occur along the roadside, as ground cover in the open oak woods, and in the broad open field which, as Fig. 3 shows, is being invaded by jack pine *(Pinus banksiana)*. A second important relic community is on the south slope of a sandstone ridge in Easton township, 13 miles north of Wisconsin Dells, at T. 16 N., R. 6 E., sec. 36 (Fig. 5). On this relic are twenty-one of the prairie species including: *Bouteloua hirsuta, Bouteloua curtipendula, Sporobolus cryptandrus,*

Fig. 3. A panorama across the relic of Dell Prairie at T. 14 N., R. 6 E., sec. 11. Note the invasion by *Pinus banksiana*.

FIG. 4. A panorama of Welch Prairie, Juneau County, as seen in 1937 showing invasion by *Pinus banksiana*. Photo by N. C. Fassett.

Andropogon scoparius, Andropogon furcatus, Elymus canadensis, Tradescantia canaliculata, Anemone patens var. *Wolfgangiana, Geum triflorum, Lespedeza capitata, Euphorbia corollata, Asclepias tuberosa, Lithospermum angustifolium, Opuntia fragilis, Liatris scariosa, Kuhnia eupatorioides, Coreopsis palmata, Ambrosia psilostachya, Chrysopsis villosa, Aster sericeus,* and *Solidago rigida.* There is some *Juniperis horizontalis* present. The old trees of bur oak *(Quercus macrocarpa)* surrounding the community are of the open grown type, indicating a former greater extent of the prairie community. Many young oaks are starting on the prairie and trembling aspen *(Populus tremuloides)* and white birch *(Betula papyrifera)* are encroaching upon the hillside. This may be a relic of a small prairie in Easton township which surveys of 1851 and the 1882 vegetational map show just to the north of the ridge on which this relic community is located. On the same ridge, a mile to the east at T. 16 N., R. 7 E., sec. 31, another group of prairie plants is persisting only on the cleared roadside where they have found a haven from the encroaching trees. Fifteen prairie species are present on this roadside; they are: *Andropogon furcatus, Andropogon scoparius, Sporobolus heterolepis, Sorghastrum nutans, Koeleria cristata, Amorpha canescens, Petalostemum candidum, Petalostemum purpureum, Desmodium illinoense, Lespedeza capitata, Euphorbia corollata, Asclepias tuberosa, Coreopsis palmata, Liatris scariosa,* and *Solidago rigida.*

Just north of the town of Grand Marsh, Adams County at T. 17 N., R. 7 E., sec. 31 and across the road in T. 16 N., R. 7 E., sec. 5 is an open field in which there are growing eighteen species of prairie plants. These appear to be relics of a prairie which surveyors recorded in 1851 and again in 1882. The species present in this field are: *Andropogon furcatus, Andropogon scoparius, Stipa spartea, Bouteloua hirsuta, Panicum virgatum, Koeleria cristata, Sorghastrum nutans, Tradescantia canaliculata, Amorpha canescens, Lespedeza capitata, Euphorbia corollata, Acerates floridana, Asclepias tuberosa, Solidago rigida, Coreopsis palmata, Ambrosia psilostachya, Hieracium longipilum,* and *Liatris scariosa.* The soil here is very dark to a depth of 10 inches. A few jack pines, hazelnut *(Corylus americana),* and scrub oaks *(Quercus ellipsoidalis)* are present. Two miles north of Grand Marsh, T. 17 N., R. 7 E., between sections 19 and 30, is another relic which has seventeen species of prairie plants growing along the road in a heavily wooded section. These include: *Andropogon furcatus, Andropogon scoparius, Stipa spartea, Panicum virgatum, Bouteloua curtipendula, Koeleria cristata, Sorghastrum nutans, Spartina pectinata, Geum triflorum, Amorpha canescens, Lespedeza capitata, Acerates floridana, Asclepias tuberosa, Euphorbia corollata, Coreopsis palmata, Hieracium longipilum,* and *Liatris scariosa.* These two relics are part of a prairie which the surveyors showed as a single large prairie in 1851 but which on the vegetational map of 1882 is shown as split into two small prairies. At present this section of the country

FIG. 5. Relic community in Adams County, T. 16 N., R. 6 E., sec. 36, on a sandy hillslope. Note the invasion by *Populus tremuloides*, *Betula papyrifera*, and *Quercus macrocarpa*.

FIG. 6. Prairie in LaCrosse County, north of Burns, showing invasion by *Quercus macrocarpa*.

FIG. 7. The Mindoro Cut, LaCrosse County, prairie relic. *Silphium laciniatum* in the left foreground. *Populus tremuloides* is invading the prairie. In the background is a hillslope on which the prairie is almost entirely gone and *Betula papyrifera* is prominent as an invader.

FIG. 8. View from the prairie hillslope at Mindoro Cut. This gives an idea of the altitude at which prairie associations may be found. Note the prairie plants in the foreground.

is fairly heavily wooded with oaks and jack pine so that this prairie shows a rather marked and constant shrinkage since 1851.

A prairie shown by the surveyors as being just north of White Creek, Adams County, appears to have entirely disappeared, at least no relic communities of prairie plants were found in the vicinity. In 1893, L. S. Cheney collected *Bouteloua curtipendula* and *Desmodium illinoense* near White Creek, probably on a relic of this prairie. Later, Professor N. C. Fassett again collected *Desmodium illinoense* near White Creek. These records and the distribution of the other species of prairie plants lead us to believe that either relic communities still persist but were undiscovered, or the relic communities have disappeared through cultivation or some other factor. At Strong's Prairie, T. 19 N., R. 4 E., sec. 36, and a larger prairie indicated by the surveyors in T. 19 N., R. 5 E. the situation is somewhat similar. Relic communities of the prairie plants no longer exist there as far as was ascertainable. In this vicinity cultivation has been rather intense and probably due to this factor the prairie plants have been largely exterminated on their original range which is shown by the records of 1851 and 1882. A few found a haven on the roadsides and poorer soils, and the maps of distribution of the prairie species reflect the presence of relics in this region.

West of Coloma is an area shown on the surveys of 1851 as prairie and on the map of 1882 as wet prairie. This was mostly in Waushara County but extended slightly into Adams County. Perhaps most of this area before drainage was sedge meadow but at the edges there appears to have been a prairie flora, as at three localities on the area are relic communities of prairie species of plants. A total of seventeen species of prairie plants still are present on this area. In Adams County at T. 18 N., R. 7 E., sec. 25 are eight species: *Andropogon scoparius, Andropogon furcatus, Stipa spartea, Sorghastrum nutans, Desmodium illinoense, Lespedeza capitata, Euphorbia corollata,* and *Asclepias tuberosa.* In Waushara County at T. 18 N., R. 8 E., sec. 19 are twelve species: *Stipa spartea, Sporobolus heterolepis, Andropogon scoparius, Andropogon furcatus, Sorghastrum nutans, Tradescantia canaliculata, Amorpha canescens, Lespedeza capitata, Euphorbia corollata, Lithospermum Gmelini, Liatris scariosa,* and *Aster multiflorus;* and in section 20 of the same township are nine species: *Andropogon furcatus, Andropogon scoparius, Amorpha canescens, Lespedeza capitata, Euphorbia corollata, Assericeus, Solidago rigida, Liatris scariosa,* and *Coreopsis palmata.*

Two other areas of Waukesha sandy loam occur in Waushara County. That in Oasis township, T. 20 N., R. 9 E., and extending north into Almond township, T. 21 N., R. 9 E., was termed "Great Prairie" and never supported a growth of timber. A smaller area near Plainfield, T. 20 N., R. 8 E., according to the "Soils Survey of Waushara County" supported a scattering growth of oaks. On Great Prairie there are not many plants in any one spot; cultivation has been too clean to leave even the roadsides as refuges

for the prairie plants. On the area of this prairie were found sixteen species of prairie plants including: *Stipa spartea, Andropogon scoparius, Andropogon furcatus, Sporobolus heterolepis, Sorghastrum nutans, Tradescantia canaliculata, Amorpha canescens, Lespedeza capitata, Asclepias tuberosa, Euphorbia corollata, Linum sulcatum, Liatris scariosa, Solidago rigida, Aster sericeus, Aster multiflorus,* and *Coreopsis palmata.* The paradox of finding more individuals of prairie species off the original prairies than on them is not so puzzling when the fact that the prairie areas were the first to be cultivated and have been under more continuous and complete cultivation is considered. This type of distribution in general holds true for the Wisconsin prairies, as the best prairie relic communities are on land which could not be cultivated easily. On the sandy soils near the original prairie area there are considerable numbers of prairie plants as may be seen by examination of the distributional maps. One of the best relic communities just at the edge of Great Prairie is on a gravel knoll at the north side of Washburn Lake, T. 21 N., R. 9 E., sec. 29. Here there are seventeen species of prairie plants: *Sporobolus heterolepis, Andropogon scoparius, Andropogon furcatus, Stipa spartea, Spartina pectinata, Panicum virgatum, Bouteloua hirsuta, Bouteloua curtipendula, Sorghastrum nutans, Koeleria cristata, Amorpha canescens, Lespedeza capitata, Lithospermum Gmelini, Acerates floridana, Euphorbia corollata, Aster sericeus,* and *Coreopsis palmata.* The prairie area around Plainfield has thirteen species of prairie plants. They are: *Stipa spartea, Sorghastrum nutans, Andropogon furcatus, Andropogon scoparius, Lespedeza capitata, Amorpha canescens, Euphorbia corollata, Linum sulcatum, Solidago rigida, Liatris scariosa, Aster sericeus, Coreopsis palmata,* and *Hieracium longipilum.*

Concentrations of prairie plants in two localities in southern Wood County were very puzzling in the field. Inquiry among the residents in the vicinity, including one of the early settlers of the region, of these concentrations gave no information as to an original prairie in those localities. Later the vegetational map of 1882 was discovered, and on it appear two small prairies in the localities which now show concentrations of prairie plants. In T. 21 N., R. 6 E., secs. 2, 11, and 14 there were fifteen species of prairie plants: *Koeleria cristata, Sporobolus heterolepis, Andropogon furcatus, Andropogon scoparius, Stipa spartea, Sorghastrum nutans, Spartina pectinata, Panicum virgatum, Tradescantia canaliculata, Lespedeza capitata, Amorpha canescens, Euphorbia corollata, Asclepias tuberosa, Liatris scariosa,* and *Coreopsis palmata.* In sections 29 and 30 there are thirteen species including: *Sorghastrum nutans, Andropogon scoparius, Andropogon furcatus, Stipa spartea, Tradescantia canaliculata, Asclepias tuberosa, Euphorbia corollata, Lithospermum Gmelini, Coreopsis palmata, Aster sericeus, Solidago rigida, Liatris scariosa,* and *Liatris cylindracea.* There are so many species and such a large number of individuals of prairie plants in this township that in the

field it was thought that a prairie relic must have been present. This hypothesis was verified by the presence of the relic on the 1882 map. Across the Wisconsin River a second prairie in Wood County has its relic community best represented in T. 21 N., R. 5 E., sec. 17. Here there are fourteen prairie species including: *Sporobolus heterolepis, Andropogon furcatus, Andropogon scoparius, Sorghastrum nutans, Stipa spartea, Tradescantia canaliculata, Amorpha canescens, Lespedeza capitata, Asclepias tuberosa, Euphorbia corollata, Coreopsis palmata, Aster sericeus, Solidago rigida,* and *Liatris scariosa.* This community of prairie species presented a similar situation to the preceding relic.

In Juneau County four relics of prairies are still in existence and a fifth has disappeared. In northern Juneau County a small prairie at T. 19 N., R. 4 E., sec. 5 was located by information given by Mr. James Blake of Necedah, long resident of the county. For some reason the surveys in both 1851 and 1882 missed this small prairie but this relic was recognized by the "old timers" as Searl's Prairie. In the center of a large cultivated area there is an old cemetery. Two tombstones bearing the dates 1862 and 1863 are in the graveyard. In this small patch which has thus been spared cultivation are sixteen species of prairie plants including: *Bouteloua hirsuta, Bouteloua curtipendula, Andropogon furcatus, Andropogon scoparius, Sporobolus heterolepis, Stipa spartea, Geum triflorum, Amorpha canescens, Opuntia Rafinesquii, Euphorbia corollata, Aster multiflorus, Aster sericeus, Solidago rigida, Coreopsis palmata, Hieracium longipilum,* and *Helianthus hirsutus.* On the nearby roadside are four additional species: *Koeleria cristata, Sorghastrum nutans, Liatris scariosa,* and *Lithospermum Gmelini.* The cemetery is grazed slightly by wandering cattle only in the autumn after the surrounding crops have been harvested, as it is unfenced, and is too small to fence and graze through the summer. The excellent preservation of this little piece of original prairie makes it very interesting.

Two prairies were reported south of Necedah by the survey of 1851 but only one is shown on the vegetational map of 1882; this is Welch's Prairie at T. 17 N., R. 4 E., secs. 6 and 7. Here in 1937 there were but few individuals of each species of prairie plant yet there was found a long list of prairie species including: *Koeleria cristata, Stipa spartea, Andropogon furcatus, Andropogon scoparius, Sorghastrum nutans, Sporobolus heterolepis, Bouteloua hirsuta, Tradescantia canaliculata, Lespedeza capitata, Baptisia leucantha, Baptisia leucophaea, Amorpha canescens, Euphorbia corollata, Acerates lanuginosa, Lithospermum Gmelini, Solidago rigida, Aster sericeus, Hieracium longipilum, Coreopsis palmata, Liatris scariosa,* and *Ambrosia psilostachya.* This is a total of twenty-one species. In 1937 the prairie showed evidence of having been ploughed previously as deep furrows were present at intervals. *Pinus banksiana* was advancing over the area and the groups of trees showed the closing in of the pine on the open space. The

older trees in each group showed the wide spreading lower branches typical of open-grown trees, while the younger ones around them showed short branches typical of close, shaded growth (see Fig. 4). There were a number of such groups of varying ages forming a series back into the deeper pine growth and showing considerable encroachment. In 1938 the entire open space and much of the pine-forested area was plowed and planted in corn. The remnant of the prairie flora was again forced to the borders of cultivation, but all of the species were still present in small numbers.

The second prairie south of Necedah and more to the east at T. 17 N., R. 4 E., secs. 2, 3, and 11 is shown by the surveys of 1851 but not in 1882. It was known as Hale's Prairie. Here are found *Koeleria cristata, Andropogon scoparius, Andropogon furcatus, Stipa spartea, Sporobolus heterolepis, Sorghastrum nutans, Tradescantia canaliculata, Lespedeza capitata, Amorpha canescens, Euphorbia corollata, Asclepias tuberosa, Lithospermum Gmelini,* and *Solidago rigida.* This is a total of thirteen, not a large proportion of the prairie species but a larger number than at many localities in the county. This "prairie" is interesting in that the area is at present all cultivated and that the edge of cultivation follows the outline of the prairie as indicated in 1851 by the surveyors. Although the soil is not a true prairie soil, it may be sufficiently richer than the surrounding land to warrant continued cultivation whereas the rest was abandoned.

South of New Lisbon at T. 16 N., R. 3 E., sec. 17 the survey of 1851 reported a prairie but the map of 1882 shows none. Here cultivation and man's "improvements" have so changed the land that probably all of the original prairie has been exterminated. The soil is still very dark, however, and there are a few plants persisting nearby.

Just north of the famous Dells of the Wisconsin River on the west side of the river there is a small relic community of prairie plants on the bank of the river at T. 14 N., R. 6 E., sec. 33. Here there is an abundant growth of *Bouteloua hirsuta, Ambrosia psilostachya,* and *Aster sericeus.* In nearby section 32 occurred *Acerates floridana* and just north in section 29 are: *Andropogon scoparius, Andropogon furcatus, Sorghastrum nutans, Koeleria cristata, Spartina pectinata, Amorpha canescens, Baptisia leucantha, Euphorbia corollata,* and *Liatris scariosa.* Just west in section 31 occur *Hieracium longipilum, Lespedeza capitata,* and *Petalostemum purpureum.* Before the dam was put in at Wisconsin Dells in 1909 this prairie must have been at the top of a steep river bluff.

In Monroe and LaCrosse Counties the relic prairie communities are of a different character from those in Juneau and Adams Counties. In the latter counties the communities are mostly on flat or nearly flat territory and are in close contact with the sandy soils on which the species have been spreading. In the former counties the relics are mainly on the south and southwestward facing slopes of the limestone bluffs on Rendzina soils. For the

most part there is no close contact with the sandy soils. These relics invariably show invasion by the forest, and indications are that this invasion has been going on for a long time, as some of the hills show an entire forest cover on the slopes which usually show prairie associations and all stages in the succession may be observed on the bluffs. Pioneers in this invasion upon the prairie are *Rhus glabra, Corylus americana, Populus tremuloides, Cornus paniculata, Betula papyrifera,* and species of *Prunus.* The prairie flora on these slopes varies from hill to hill, being rich on some and poor on others.

In Monroe County the following were examined. West of Kendall at T. 15 N., R. 1 E., sec. 18 there were but eight species including: *Bouteloua curtipendula, Koeleria cristata, Anemone patens* var. *Wolfgangiana, Anemone cylindrica, Amorpha canescens, Petalostemum purpureum, Euphorbia corollata,* and *Coreopsis palmata.* But few individuals of each species were left as the bluff was heavily grazed and badly eroded. The Pasque flower (*Anemone patens* var. *Wolfgangiana*) was preserved by growing beneath a brush pile. At another bluff 5 miles west of Norwalk, T. 16 N., R. 3 W., sec. 27, there were thirteen species: *Bouteloua hirsuta, Bouteloua curtipendula, Koeleria cristata, Sporobolus heterolepis, Andropogon scoparius, Sorghastrum nutans, Anemone patens* var. *Wolfgangiana, Amorpha canescens, Baptisia leucantha, Petalostemum purpureum, Scutellaria parvula* var. *ambigua, Helianthus hirsutus,* and *Solidago rigida.* This bluff was heavily pastured and the prairie left only at the extreme edge where the angle is too sharp for the cattle to feed. There is considerable invasion by *Rhus glabra, Betula papyrifera, Corylus americana, Quercus macrocarpa, Quercus velutina,* and *Carya ovata.* At 4 miles northwest of Tunnel City, T. 18 N., R. 2 W., sec. 10, the conditions are about the same with heavy pasturing and invasion by *Rhus glabra* and *Betula papyrifera.* Thirteen species also were represented at this locality. They include: *Bouteloua curtipendula, Sporobolus heterolepis, Sporobolus vaginiflorus, Andropogon scoparius, Andropogon furcatus, Anemone patens* var. *Wolfgangiana, Petalostemum purpureum, Amorpha canescens, Euphorbia corollata, Aster tardiflorus, Aster sericeus, Solidago rigida,* and *Talinum rugospermum.*

One other place in Monroe County deserves especial notice, not because it is definitely known as a relic but because at this one location there is a large assemblage of species. This is at about one-half mile east of the Tunnel City station, T. 18 N., R. 2 W., sec. 25, on an abandoned railroad grade. Here there are twelve species of prairie plants including: *Sporobolus heterolepis, Sorghastrum nutans, Andropogon scoparius, Andropogon furcatus, Amorpha canescens, Baptisia leucophaea, Petalostemum purpureum, Petalostemum candidum, Euphorbia corollata, Coreopsis palmata, Liatris scariosa,* and *Solidago rigida.* These plants were probably brought in on the railroad, possibly in hay, and became established as a thriving community which may have served as a reservoir from which further spread of the species took

place. Several prairie species are also found on the west side of the tunnel, among them being: *Andropogon scoparius, Andropogon furcatus, Lespedeza capitata,* and *Liatris scariosa.* These occur in greatest abundance along the railroads on the embankments and between the railroad lines on the disturbed soil.

LaCrosse County prairie communities are mainly located on the south and southwest facing hillsides. The slopes also show forest invasion upon the prairie. The prairie relics shown on the maps indicate all of the bluffs observed to have prairie on them. Close examination of several of these was made and the data on these follow.

At T. 18 N., R. 5 W., sec. 33, 4 miles north of Burns, the prairie is very heavily invaded by *Cornus paniculata, Quercus macrocarpa, Carya ovata,* and *Celastrus scandens* (Fig. 6). Two young poplars *(Populus tremuloides)* may also be counted among the invaders. Despite this invasion, there were eighteen species of prairie plants present on the prairie which is a south-facing slope. This was the only prairie observed in which bur oak was a prominent early invader. The prairie plants present are: *Sorghastrum nutans, Bouteloua curtipendula, Andropogon scoparius, Andropogon furcatus, Sporobolus heterolepis, Anemone cylindrica, Rosa heliophila, Petalostemum purpureum, Amorpha canescens, Lithospermum canescens, Euphorbia corollata, Solidago rigida, Liatris scariosa, Liatris cylindracea, Kuhnia eupatorioides, Aster sericeus, Helianthus hirsutus,* and *Coreopsis palmata.*

At Mindoro Cut, T. 17 N., R. 6 W., sec. 4 (Figs. 7 and 8), fifteen species are present on the south facing side of the hill through which the cut was made. These are: *Bouteloua curtipendula, Bouteloua hirsuta, Andropogon furcatus, Stipa spartea, Sorghastrum nutans, Sporobolus heterolepis, Amorpha canescens, Petalostemum purpureum, Euphorbia corollata, Solidago rigida, Liatris cylindracea, Silphium laciniatum, Coreopsis palmata, Aster sericeus,* and *Helianthus scaberrimus.* Invading this prairie are *Cornus paniculata, Populus tremuloides,* and *Betula papyrifera.*

West of this community, southeast of Mindoro, T. 18 N., R. 6 W., sec. 31, is another limestone bluff with but nine species: *Bouteloua hirsuta, Bouteloua curtipendula, Sorghastrum nutans, Andropogon scoparius, Anemone patens* var. *Wolfgangiana, Amorpha canescens, Petalostemum purpureum, Lithospermum Gmelini,* and *Aster sericeus.* This bluff has as invaders: *Rhus glabra, Betula papyrifera,* and one *Carya ovata.*

Five miles north of West Salem on County highway C, T. 17 N., R. 6 W., sec. 11, is another slope, facing south, which has the largest number of prairie species of any relic examined in LaCrosse County, a total of nineteen. *Bouteloua hirsuta, Bouteloua curtipendula, Sporobolus heterolepis, Andropogon furcatus, Andropogon scoparius, Sorghastrum nutans, Amorpha canescens, Petalostemum purpureum, Petalostemum candidum, Euphorbia corollata, Agalinis aspera, Scutellaria parvula* var. *ambigua, Aster sericeus, Sil-*

phium laciniatum, Kuhnia eupatorioides, Coreopsis palmata, Solidago rigida, Liatris scariosa, and *Lepachys pinnata* are on this slope. Near the top is a long abandoned portion of roadway and the prairie plants are established on this as well as on the slope proper. The top of the hill and the northern exposure was under cultivation. The prairie is very heavily invaded by *Rhus glabra, Betula papyrifera, Corylus americana,* and *Populus tremuloides* (Fig. 9).

The bluffs along the Mississippi River have their west and south facing slopes usually covered with prairie communities. Characteristic of this bluff distribution is one observed 3 miles north of Holmen (Fig. 10). This limestone bluff is pastured heavily wherever the cattle can walk, mainly at the top and the base, but where the cattle do not readily reach is a typical prairie community of nine species: *Bouteloua hirsuta, Bouteloua curtipendula, Koeleria cristata, Amorpha canescens, Petalostemum purpureum, Euphorbia corollata, Lithospermum angustifolium, Coreopsis palmata,* and *Kuhnia eupatorioides. Sporobolus heterolepis* is to be found along the roadside not far from this bluff. The prairie on the bluff has some prickly ash *(Xanthoxylum americanum)* and some wolfberry *(Symphoricarpos occidentalis)* growing on it.

Brice Prairie, as named by the earlier settlers, and indicated on the soils map of LaCrosse County in T. 17 N., R. 8 W. is very interesting. It has been heavily cultivated so that not much was expected in the way of a relic flora upon it. But at T. 17 N., R. 8 W., sec. 14 along the roadside are a few plants of *Bouteloua curtipendula* and *Stipa spartea.*

Right off Brice Prairie just south of Midway, T. 17 N., R. 7 W., sec. 30, on one of the sand terraces of the Mississippi River, between the railroad and the main highway is an excellent prairie community which has escaped grazing as well as cutting by reason of its location between the two avenues of traffic (Fig. 11). Fourteen species are here represented: *Bouteloua hirsuta, Sporobolus cryptandrus, Panicum virgatum, Andropogon scoparius, Andropogon furcatus, Koeleria cristata, Anemone patens* var. *Wolfgangiana, Amorpha canescens, Petalostemum purpureum, Euphorbia corollata, Lithospermum Gmelini, Aster sericeus, Solidago rigida,* and *Kuhnia eupatorioides.* The location of this community on the sand terrace along the Mississippi River is similar to the prairie community to be seen on the sand terraces at the foot of Lake Pepin where the Chippewa River enters the Mississippi River.

In the southern part of the county another representative bluff on limestone may be seen four miles southeast of Shelby at T. 15 N., R. 6 W., sec. 28 (Fig. 13). Sixteen species are represented on this bluff, including: *Bouteloua curtipendula, Andropogon scoparius, Andropogon furcatus, Sorghastrum nutans, Amorpha canescens, Petalostemum candidum, Petalostemum purpureum, Solidago rigida, Coreopsis palmata, Euphorbia corollata, Litho-*

Fig. 9. Prairie five miles north of West Salem, LaCrosse County. Note strong invasion by *Rhus glabra* and *Populus tremuloides*. Bur oaks *(Quercus macrocarpa)* are growing at the top of the hill.

Fig. 10. A bluff north of Holmen, LaCrosse County. The prairie species are found on the steep unpastured slope just above the long horizontal rock exposure which forms the upper part of the cliff.

Fig. 11. A prairie community on the side of a sand terrace of the Mississippi River near Midway, LaCrosse County. A railroad is below the terrace and a main highway above so the relic has escaped grazing. The steep slope and sandy soil do not permit cultivation.

Fig. 12. *Euphorbia corollata* by a roadside in Adams County showing initial invasion along the road and a scattering invasion into the adjacent abandoned fields from the plants along the roadside.

spermum angustifolium, Scutellaria parvula var. *ambigua, Liatris cylindracea, Liatris scariosa, Aster sericeus,* and *Helianthus scaberrimus.* Invaders include *Rhus glabra, Betula papyrifera,* and *Populus tremuloides* with the trees creeping up the slope against the prairie rather rapidly as shown by the broad edge band of *Populus* in which the sizes taper down to the youngest in the prairie. *Silphium perfoliatum* grows in the low ground near a spring at the foot of the hill.

FIG. 13. A prairie hillside near Shelby, LaCrosse County. This is a typical "goat" prairie with the prairie community growing on a slope of high angle "which a goat can climb with more ease than a man."

In Portage County there are several possible relic prairies. At Lake Emily near Amherst Junction *Bouteloua curtipendula* was collected by J. H. Schuette on August 21, 1891. This community was not relocated but in this township, T. 23 N., R. 9 E., concentrations of twelve of the prairie species occur. *Gentiana puberula* is found in T. 23 N., R. 10 E., sec. 18, also near Lake Emily. Along the railroad near Custer, T. 23 N., R. 9 E., sec. 3, there are thirteen species of prairie plants in what appear to be prairie relic communities on gravelly soil. They include: *Sporobolus heterolepis, Stipa spartea, Andropogon furcatus, Andropogon scoparius, Koeleria cristata, Lespedeza capitata, Amorpha canescens, Euphorbia corollata, Gentiana puberula, Aster sericeus, Solidago rigida, Coreopsis palmata,* and *Liatris scariosa.* Just west of Plover and south of the bend in the Wisconsin River there may be a possible relic community although the railroad line runs through here and there is a possibility that the large concentrations of prairie plants in this vicinity may be due to invasion via the railroad. Neither of these two possible relic communities of prairie plants is indicated on the vegetational map of 1882. Just west of Portage County, in Waupaca County in T. 23 N., R. 11 E. is an important prairie relic similar to the "Great Prairie" in Oasis township in Waushara County. This is not shown on the maps accompanying this report but provides a source for the invasion of prairie plants into eastern Portage County. Along the railroad west of Amherst there are several concentrations of prairie plants which possibly are remnants of this prairie or invasions from it.

GENERAL DISCUSSION

Evidence from several sources points to a former greater extent of prairie in Wisconsin. Gleason (1922) shows that relic communities are evi-

dence of a retreating migration of the prairie to the westward. Such communities are common in central Wisconsin. There seems to be evidence for at least the former existence of a prairie relic in Marinette County to the northeastward; and specimens of such prairie plants as *Andropogon furcatus, Lespedeza capitata, Silphium terebinthinaceum, Solidago rigida,* and *Sporobolus cryptandrus* collected by J. H. Schuette on the shores of Green Bay at Fort Howard, Brown County, in 1886 and 1890 bespeak the former presence of a relic prairie in that locality also. A. W. Schorger (1937) in discussing the former range of the buffalo in Wisconsin shows that within historical times the prairie in this state had a much wider range than the present. He is of the opinion that prairie fires, set by the Indians annually, maintained broad open patches of prairie as far north as Lake Winnebago in the eastern part of the state. The limit of the broader prairies probably can be correlated roughly with the range of the bison. There is ample evidence in the form of surveyors reports, a vegetational map of Wisconsin made in 1882 and present relic communities to justify the conclusion that smaller patches of prairie existed at the time of settlement of this region beyond the almost continuous prairies on which the buffalo ranged.

Since settlement of central Wisconsin, beginning in the eighteen-fifties, the prairie areas have been steadily retreating. Cultivation of the prairie soils which were rich and easily tilled has of course largely exterminated the prairie floras on these tracts. Aside from this factor, however, the prairie relic communities which have remained comparatively undisturbed, show a marked shrinkage. The forest is invading even the southwestern bluff exposures along the Wisconsin and Mississippi Rivers and their tributaries; places which contain among the best prairie relics in the state. The discussion of the prairie relics in this paper gives some of the evidences of this invasion of the bluffs. Welch Prairie, south of Necedah, in 1937 just before it was plowed and planted showed invasion by jack pine *(Pinus banksiana)*. The same is true of Dell Prairie in those portions which have not recently been disturbed by cultivation. A slightly more humid climate might account for this invasion by forest but so also might the cessation of annual burning by the Indians. If the climate is humid enough to support tree growth but the trees are annually burned off, the forest does not get a chance to compete successfully with the prairie. The effect of fires in extending the prairie in the midwest has also been discussed by Gleason (1913). When the annual burning ceases, then the trees may invade the artificially maintained prairies. There is no doubt that the fires favor the prairie species and harm the trees but whether they are the main factor in the spreading of the prairie is still open to question. A comparison of surveyors records of 1851 with the 1934 Forest and Cover Maps of Juneau County compiled by J. S. Bordner *et al.* shows that the jack pine has advanced several miles southward in that county (Fig. 14). The range was checked by field observations in 1937 and this

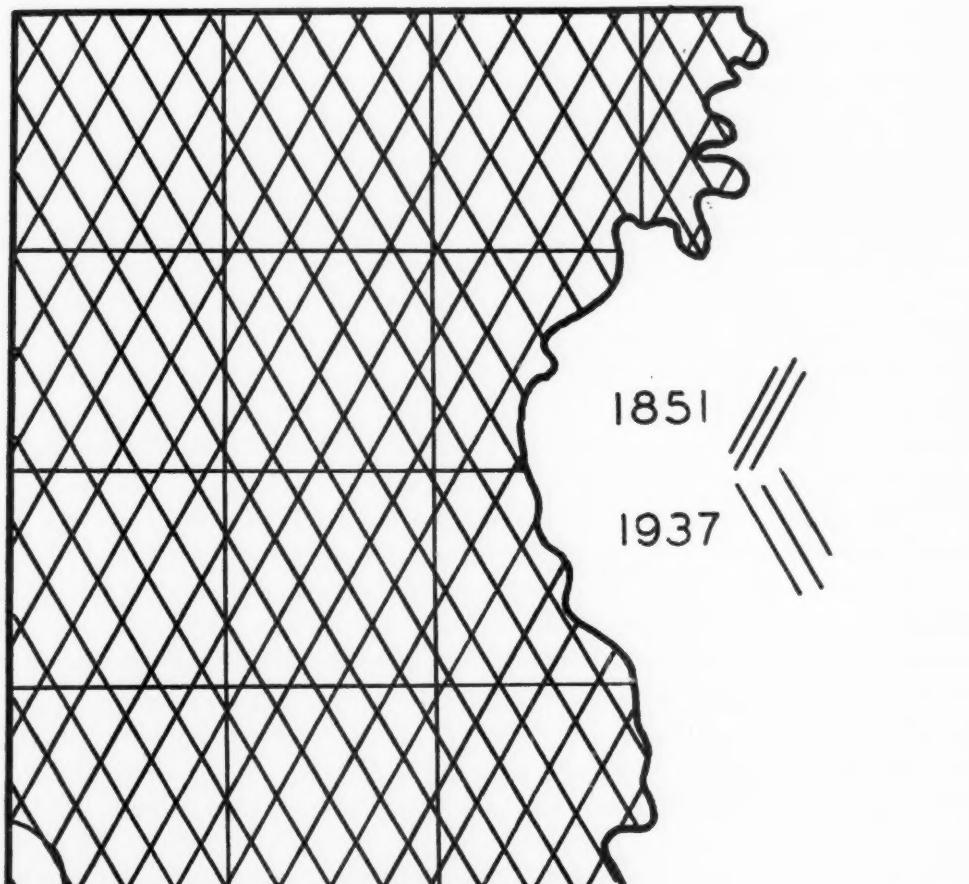

FIG. 14. The range of jack pine *(Pinus banksiana)* in Juneau County, Wisconsin, in 1851 and 1937.

advance is very apparent; as a matter of fact the jack pine extends south into Sauk County near Spring Green on the sand plains there and on a single bluff of sandstone in Iowa County. Here then is further evidence for an advance of the northern forests.

Studies on abandoned fields in Juneau County point to about the same conclusions. The prairie species come into the fields in numbers at from 9 to 10 years after abandonment and reach a maximum about 15 years after the field has been abandoned. However, the prairie plants decline in importance and by 35 years after abandonment the forest has moved in on the fields, represented at first by jack pine and aspen but later the oaks also become important. This may be compared with Shimek's (1925) observations on the prairie in Iowa. Here he found that the prairie had become established after 10 years but that 30 years were required for a complete establishment. Here in Wisconsin in Juneau County on the sandy soils at the very edge of the range of the prairie species, the establishment never is completed and the forest becomes the dominant.

These facts point to the conclusion that the prairie flora is rapidly being exterminated by the forest and by the activity of man. In order to have communities of prairie plants for field study, not only must some of the few remaining relic communities be acquired but succession toward forest must be retarded or prevented.

While the original prairies are disappearing, some of the members of the prairie flora are finding a haven on the soil disturbed by man in the counties surveyed for this report and are maintaining themselves along roadsides, railroads, and in abandoned fields (Figs. 12 and 15).

It is a well-known fact that species of plants vary in their ability to spread and invade. Among the various prairie plants found in central Wisconsin this variability may also be noted. *Bouteloua hirsuta* for example may be termed a conservative species as it is found only on the relics of former prairies (Fig. 16). L. S. Cheney collected it near Quincy, Adams County, in 1893 probably on a relic of the prairie in T. 16 N., R. 5 E., but it no longer grows there. In LaCrosse and Monroe Counties it grows on the steep hillside or "goat" prairies and also on the sand terraces of the Mississippi River. In the central sand plain it still grows on some of the relics but in others it has been exterminated. Probably extermination will be the fate of all of the conservative prairie species in central Wisconsin as the encroachment of the forest and the activities of man gradually eliminate such relics as are left. Prairie species with distributions in central Wisconsin similar to that of *Bouteloua hirsuta* in that they grow only on prairie relics are *Agalinis aspera, Anemone cylindrica, Ambrosia psilostachya, Bouteloua curtipendula, Gentiana puberula, Kuhnia eupatorioides, Lepachys pinnata, Lithospermum angustifolium, Opuntia fragilis,* and *Silphium laciniatum.* Others which have spread along roadsides, railroads, and in abandoned fields may be termed the

less conservative species. In considering the invasion of these species in the central sand plain of Wisconsin it is necessary to weigh four possibilities: (1) an invasion from the west, (2) an invasion from the south, (3) an invasion with the prairie relic communities as foci, and (4) a combination of an invasion from the relic communities with an invasion from the west or south.

An invasion from the west in LaCrosse County and along the sands through Monroe County into Juneau and Adams Counties may be eliminated on the grounds that such an invasion would have left many more plants and a heavier concentration of communities of these plants in northern LaCrosse and Monroe Counties than are present.

When the ranges of such plants as *Andropogon scoparius* (Fig. 22), *Coreopsis palmata* (Fig. 23), *Euphorbia corollata* (Fig. 24), and *Lespedeza capitata* (Fig. 25), are first considered, they appear to present good evidence for an invasion of the prairie plants from the south via the Wisconsin River Valley. But should not these ranges be interpreted in the light of the ranges of some of the more conservative species? In addition to those species which have already been mentioned as being confined to the relic communities there is a group of species whose distributions show what appears to be a limited spread from some of the relic communities. Such distributions support the third or fourth hypothesis rather than either of the first two. *Hieracium longipilum* (Fig. 17), and *Sporobolus heterolepis* (Fig. 18), show this type of distribution. Other species of prairie plants which have shown but slight migration from the relic communities are *Acerates floridana, Acerates lanuginosa, Anemone patens* var. *Wolfgangiana, Desmodium illinoense, Geum triflorum, Liatris cylindracea, Lithospermum Gmelini, Petalostemum candidum*, and *Petalostemum purpureum*.

A third group of species have migrated farther from the relics but show very marked concentrations of distribution near the relics. Four species are very good examples of this type of distribution; they are *Aster sericeus* (Fig. 19), *Liatris scariosa* (Fig. 20), *Solidago rigida* (Fig. 21), and *Stipa spartea*. In Marinette County in northeastern Wisconsin, T. 32 N., R. 19 E., secs. 18 and 19, there is a similar concentration of prairie plants which suggests the possibility of the existence of a relic of the former greater extent of prairie although the species present may have been introduced in hay used in feeding the horses used in lumbering. Associated with *Aster sericeus*, which is quite common, are *Andropogon furcatus, Koeleria cristata, Liatris scariosa*, and *Liatris cylindracea*. Lumbering is known to have played a part in the introduction of prairie plants in northern Wisconsin. On the site of the now extinct lumbering town of Lenawee, Chas. Goessl collected a specimen of *Euphorbia corollata* in 1917. In 1937 *Euphorbia corollata* no longer occurred near the site of the town although a few plants of *Spartina pectinata, Panicum virgatum*, and *Ambrosia psilostachya* were still present. Probably the

Fig. 15. A roadside in Adams County with *Euphorbia corollata* on the recently graded strip near the road and *Liatris scariosa* in the portion undisturbed probably for several years.

spurge was introduced in the hay for the horses used in the lumbering town and afterwards disappeared when the ground was no longer sufficiently disturbed to provide a suitable environment for it. Studies on abandoned fields in Juneau County have shown that the prairie species are most vigorous between 15 and 20 years after the field has been abandoned. A similar instance of this type of introduction is an isolated community of *Solidago rigida* and *Sorghastrum nutans* in an abandoned field in Iron County from which Dr. N. C. Fassett collected specimens in 1928. In 1937 this colony could no longer be located. In Bayfield County by Lake Wiehe, T. 47 N., R. 8 W., sec. 18, Dr. Fassett had noticed a community of prairie plants on an old roadbed. When this locality was revisited in 1937 the road had been relocated several yards off to the east and the prairie plants had been exterminated on the old road by invasion of the northern flora but had found the disturbed soil of the newer road suitable for their own invasion. *Andropogon furcatus, Panicum virgatum, Coreopsis palmata, Petalostemum purpureum,* and *Lepachys pinnata* were the prairie species growing in this community.

If the ranges of the more vigorously invading species are examined, keeping in mind the ranges of the four species, *Stipa spartea, Aster sericeus, Liatris scariosa,* and *Solidago rigida,* it will be noticed that these also show a concentration of distribution near the relic communities. This represents not only a greater number of communities but in many cases seen in the field, the new communities are larger as the relic is approached. Such ranges suggest a spread from the relic communities rather than a general invasion of more vigorous individuals from the south which would overrun the supposedly more conservative individuals of the same species left in the relics. In the species which we may call the more vigorous, invasion from each of the relics has taken place to such an extent that the range of the species becomes almost continuous, the gaps between the relics being filled with invading plants. The evidence for the invasion having occurred with the relics as foci of infection thus becomes indistinct. This type of distribution

is shown by *Andropogon scoparius* (Fig. 22), *Coreopsis palmata* (Fig. 23), *Euphorbia corollata* (Fig. 24), and *Lespedeza capitata* (Fig. 25). Other species with similar distribution in central Wisconsin are *Koeleria cristata* and *Sorghastrum nutans.*

It may be suggested that the reason that more of each of the prairie species may be found on the sands of Juneau and Adams Counties than on the corresponding soils of Monroe and LaCrosse Counties, with the possible exception of the sands near Brice's Prairie in LaCrosse County, is the fact that the relic communities in these two counties are in close contact with the sandy soils on which the invasion is taking place and that the invasion may thus be facilitated. In Monroe and LaCrosse Counties the relic communities are located on bluffs rather remote in most cases from the soils on which the invasion is taking place, with the result that infection is not as continuous nor as dense.

Some species such as *Andropogon furcatus* and *Tradescantia canaliculata* are not quite as clear cut in their distribution. They occur on the heavier as well as the lighter soils and under varying conditions of soil moisture. However, even these species show some degree of concentration near the prairie relic communities in some places. *Panicum virgatum, Spartina pectinata, Baptisia leucantha, Baptisia leucophaea,* and *Asclepias tuberosa* all show such questionable ranges. Perhaps a thorough study of these species in regard to their requirements and the conditions present where they are found might explain their ranges better. More data on the physiology and environment of the prairie species are needed.

SUMMARY

Historical evidence and the presence of relic communities of prairie plants show that the prairie in Wisconsin once had a much wider range than at present. As the prairie receded westward and the forest advanced, small relic communities of prairie plants were left in central Wisconsin. Some of these have been exterminated by cultivation, but portions of others are still present. These relics are still being invaded by the forest and unless some of them are acquired and the forest succession halted artificially, the prairie will disappear from Wisconsin.

While the relics themselves and the most conservative species are disappearing, some of the prairie plants are spreading from the relic communities onto the sandy soils of central Wisconsin. This spread is all upon areas disturbed by the activities of man, such as roadsides, railroad rights-of-way, and abandoned fields. The succession on such places, as determined by studies of abandoned fields, is from weed flora the first few years, with rapid changes in the succession, to prairie plants, which appear in numbers from 9 to 10 years after abandonment, reach a maximum at about 15 years, and then finally decline. Then the forest represented by jack pine and aspen and later also oak supersedes the prairie plants.

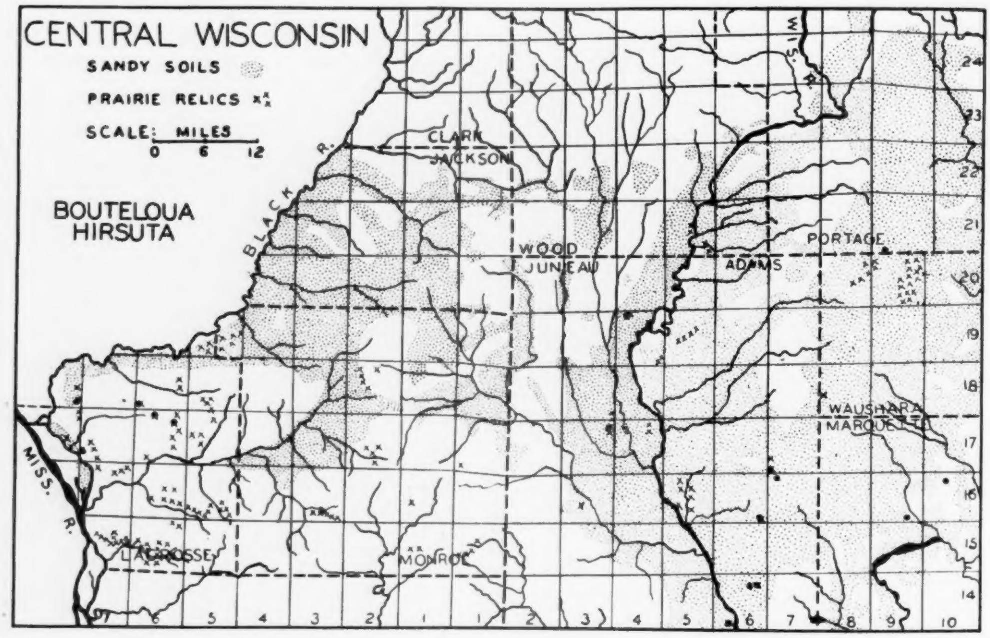

Fig. 16. Distribution of *Bouteloua hirsuta* in central Wisconsin.

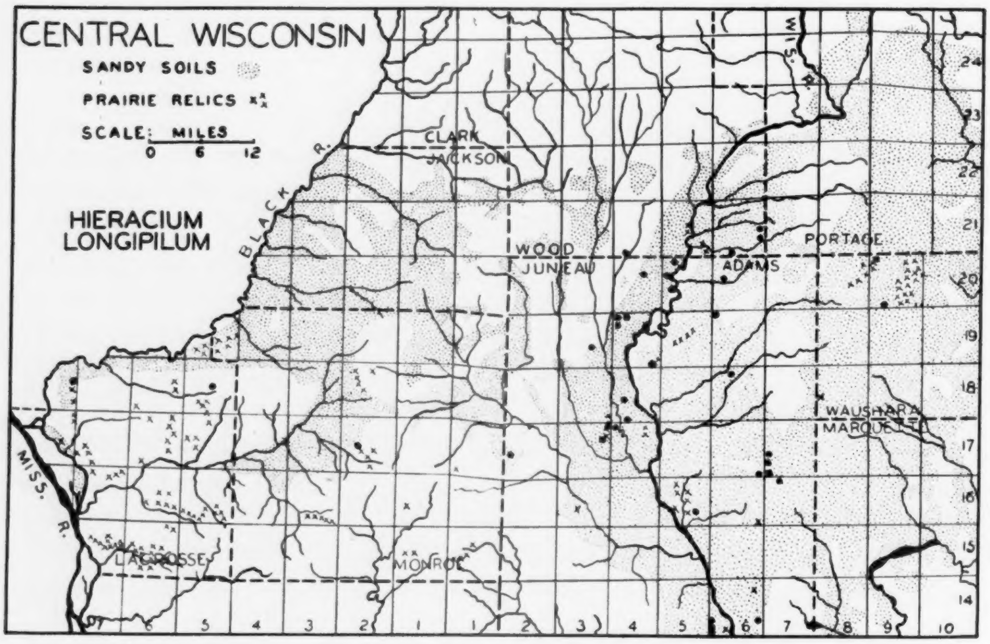

Fig. 17. Distribution of *Hieracium longipilum* in central Wisconsin.

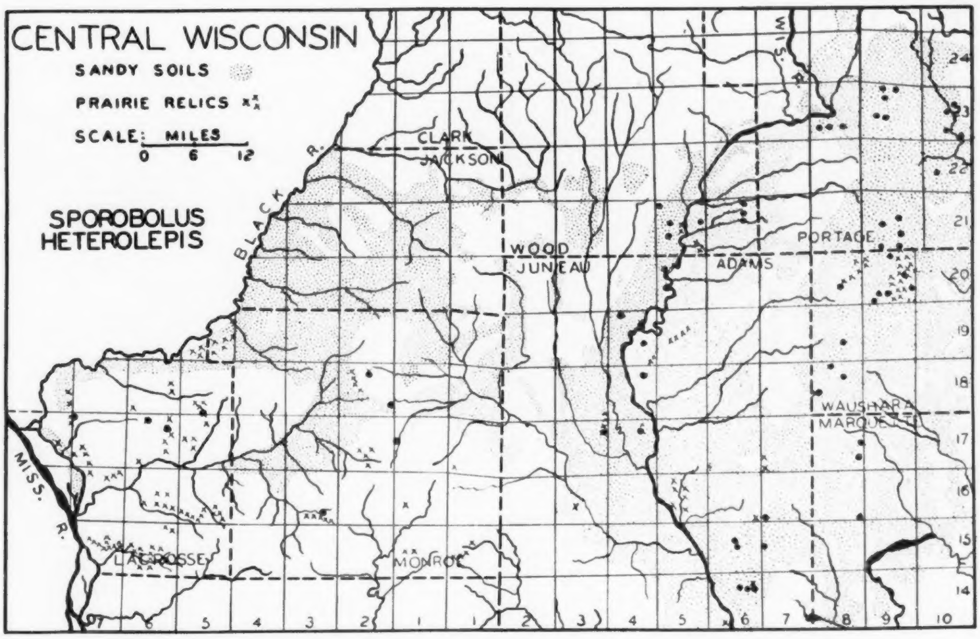

Fig. 18. Distribution of *Sporobolus heterolepis* in central Wisconsin.

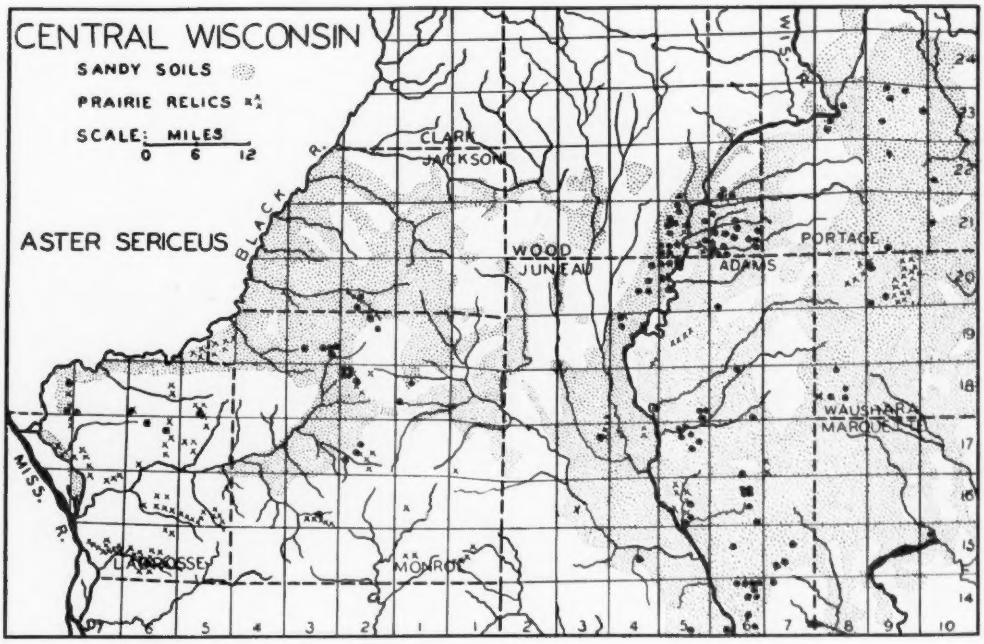

Fig. 19. Distribution of *Aster sericeus* in central Wisconsin.

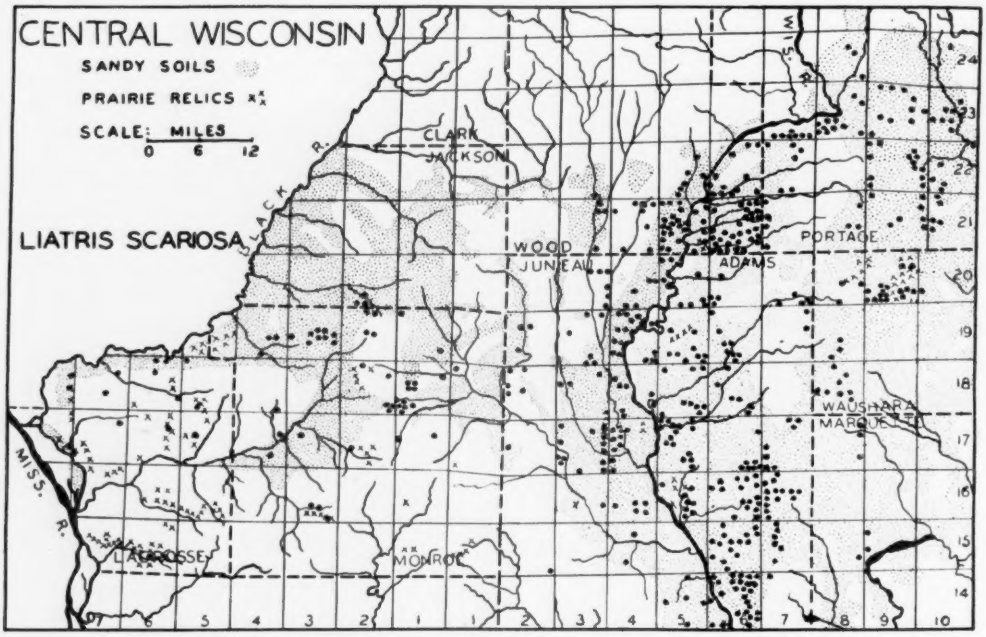

Fig. 20. Distribution of *Liatris scariosa* in central Wisconsin.

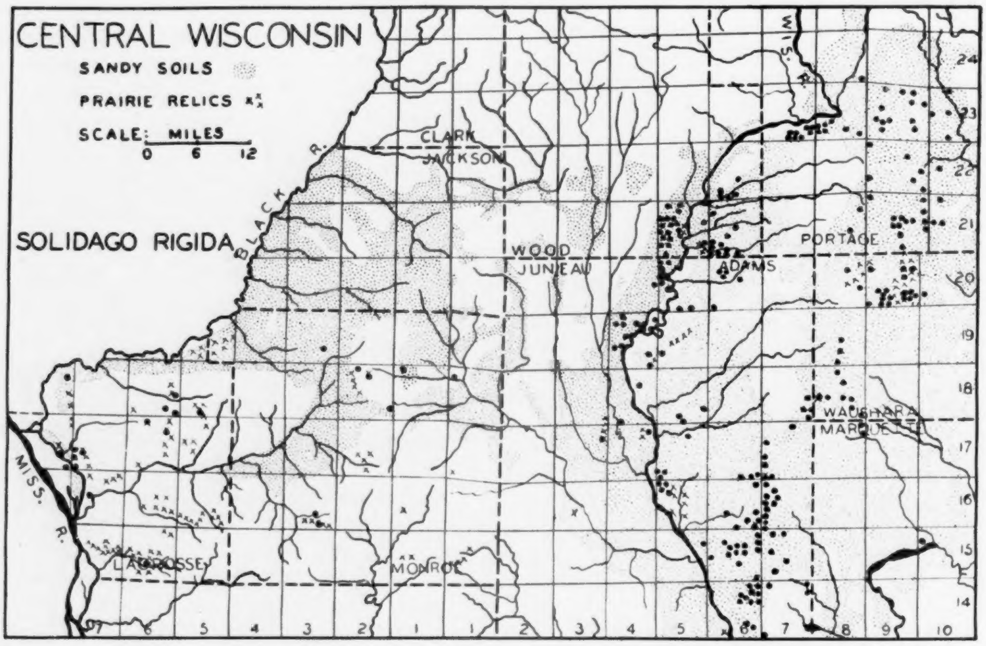

Fig. 21. Distribution of *Solidago rigida* in central Wisconsin.

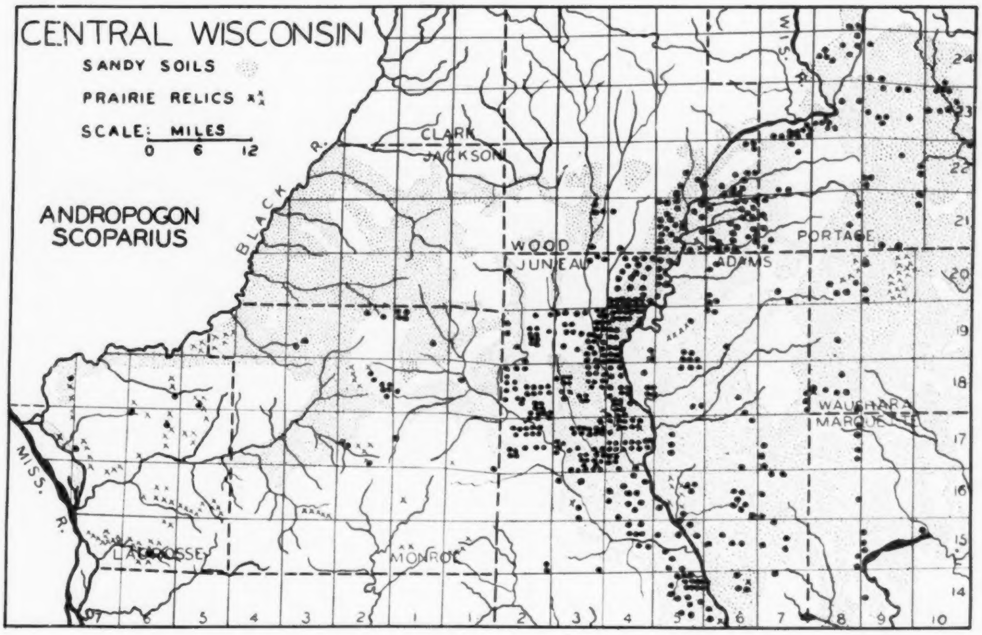

Fig. 22. Distribution of *Andropogon scoparius* in central Wisconsin.

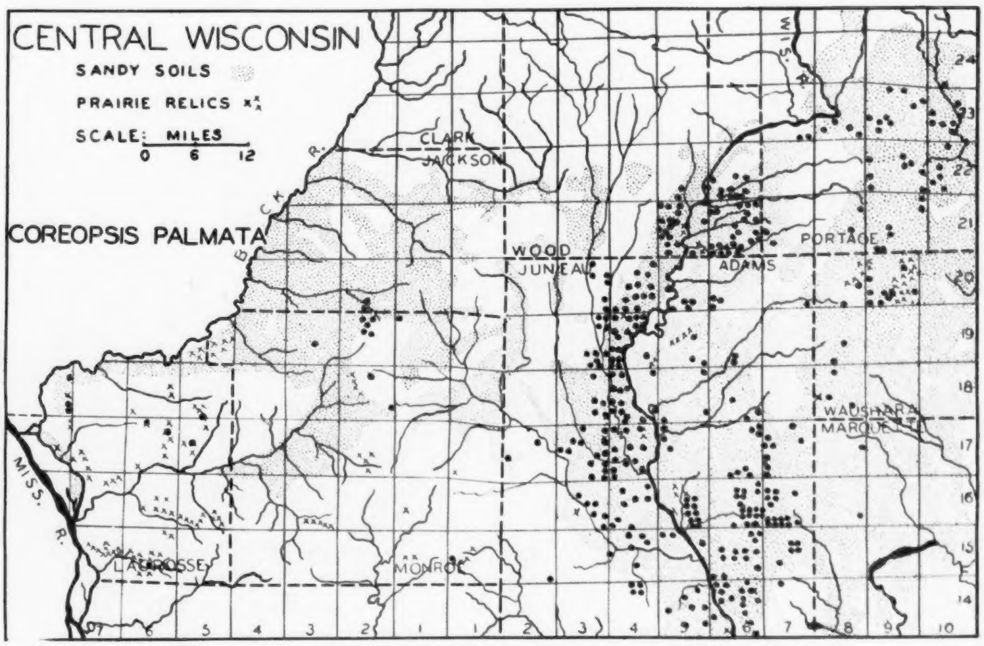

Fig. 23. Distribution of *Coreopsis palmata* in central Wisconsin.

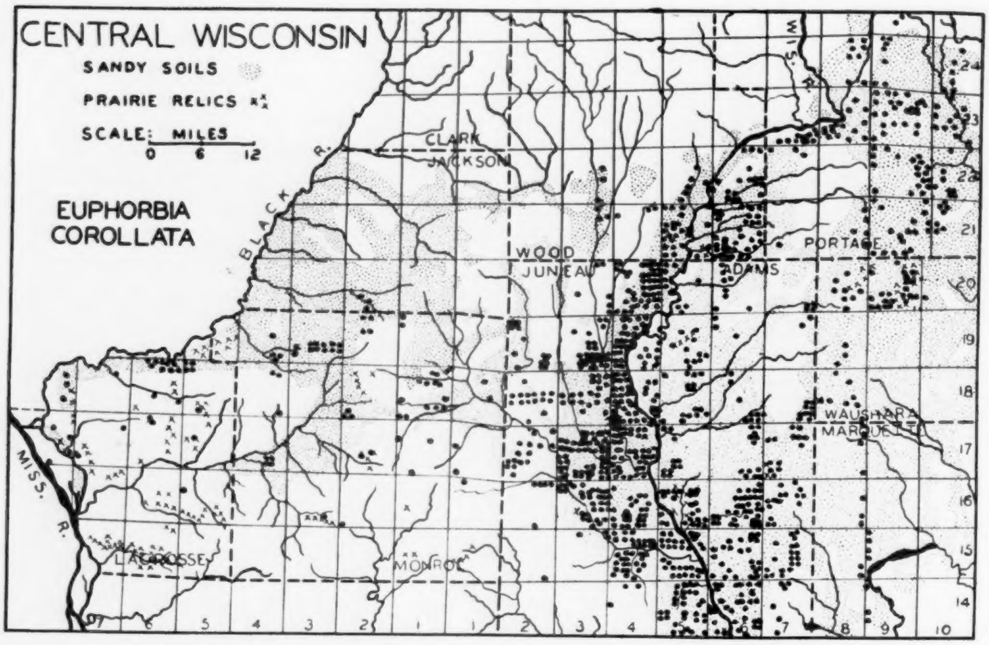

Fig. 24. Distribution of *Euphorbia corollata* in central Wisconsin.

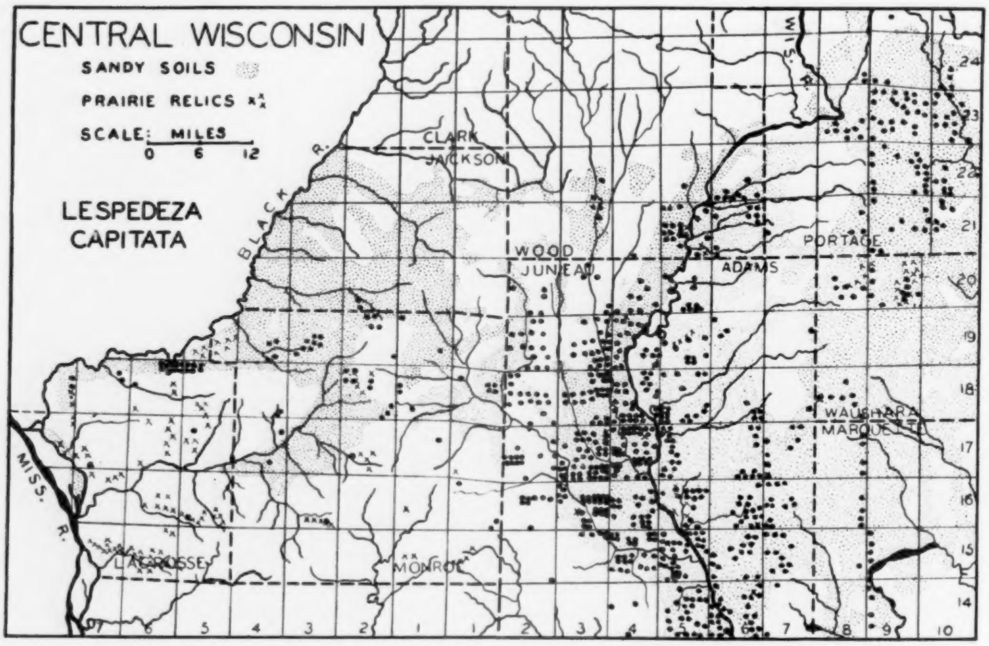

Fig. 25. Distribution of *Lespedeza capitata* in central Wisconsin.

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